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LIFE HISTORIES OF COMMERCIALY IMPORTANT TROPICAL
SHARKS FROM THE GREAT BARRIER REEF WORLD HERITAGE
AREA

Thesis submitted by
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in August 2011

For the degree of Doctor of Philosophy
in the School of Earth & Environmental Sciences
James Cook University
Townsville



Supervisors
Colin Simpfendorfer
Andrew Tobin

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CONTRIBUTIONS OF OTHERS TO THIS THESIS

Jenny Ovenden, Jessica Morgan & Raewyn Street (Department of Employment, Economic Development and Innovation, Queensland)

- Molecular analysis of blacktip shark samples (Chapter 5)

Julia Davies and Jason Stapley (Department of Employment, Economic Development and Innovation, Queensland)

- Fisheries observer data for the Queensland East Coast Inshore Finfish Fishery (Chapter 2)

Wayne Sumpton (Department of Employment, Economic Development and Innovation, Queensland)

- Raw fecundity data for hammerhead sharks from the Queensland Shark Control Program (Chapter 7)

Jonathan Werry (Griffith University)

- Eleven *Sphyrna lewini* vertebrae samples (Chapter 4)

Will Macbeth and Pascal Geraghty (New South Wales Department of Primary Industries and Fisheries and Macquarie University)

- Vertebrae samples and reproductive data from 43 *S. lewini* and 12 *S. mokarran* (Chapter 4)

Kevin Vincent (Queensland Shark Control Program)

- Vertebrae samples from one *S. lewini* and one *S. mokarran* (Chapter 4)

Rowan Gibbs (Department of Employment, Economic Development and Innovation, Queensland)

- Vertebrae samples from one *S. mokarran* (Chapter 4)

Adrian Gutteridge (University of Queensland)

- Vertebrae and reproductive samples from fourteen *S. lewini* and seven *S. mokarran* including an individual injected with calcein for age validation (Chapter 4)

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- Chapter 3. Harry, A.V., Simpfendorfer, C.A., Tobin, A.J., **2010**. Improving age, growth, and maturity estimates for aseasonally reproducing chondrichthyans. *Fish. Res.* 106, 393-403.
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PRESENTATION OF RESEARCH FROM THIS THESIS

Research from this thesis was presented at the following conferences or forums:

- 2008. Poster presentation, Oceania Chondrichthyan Society. “Reproductive biology of Queensland’s tropical inshore Carcharhiniformes. Preliminary findings on six commercially important species and a comparison with northern Australian populations.”
- 2008. Oral presentation. School of Earth & Environmental Sciences Postgraduate Research Conference. “The life of the scalloped hammerhead, *Sphyrna lewini*, in Queensland waters.”
- 2009. Oral presentation. School of Earth & Environmental Sciences seminar series. “The life history of hammerhead sharks in the GBRWHA.”
- 2009. Oral presentation. 8th Indo Pacific Fish Conference. “The life history of two hammerhead species in the GBRWHA.”
- 2009. Poster presentation. Marine and Tropical Scientific Research Facility Conference. “The life history of two hammerhead species in the GBRWHA.”
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- 2010. Oral presentation. Australian National Network in Marine Science “Assessing and mitigating the risk of overexploitation to tropical Carcharhiniform sharks posed by inshore fisheries.”
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Abstract

Elasmobranchs (sharks and rays) are captured by a number of coastal fisheries operating across tropical northern Australia. As they are typically not targeted by these fisheries, accurate data on their biology and composition in the catch is often lacking, impeding sustainable use and management. Effective fisheries management is particularly important for elasmobranch populations as they often have biological characteristics that make them susceptible to overfishing and slow to recover once overfishing has occurred.

The largest extractive fishery for sharks in Queensland waters is the East Coast Inshore Finfish Fishery (ECIFF). In 2011 the commercial gillnet sector of this fishery had a total allowable catch (TAC) of 600 t, although catches rates were as high as 1400 t.yr⁻¹ in 2004, prior to the introduction of a TAC. The large geographic area, relatively low value, and disparate nature of the ECIFF mean monitoring of the catch is difficult. Yet as the fishery occurs predominantly within the Great Barrier Reef World Heritage Area (GBRWHA), it is closely scrutinised by the general public and stakeholder groups (e.g. marine park management, tourism, conservation groups). Effective and defensible science-based management is therefore especially important for the ECIFF.

Between 2006 and 2009 an onboard vessel observer survey program was undertaken on the ECIFF with the goal of obtaining biological information that could be used to help manage, in particular, the shark component of the fishery. The observer survey was the most extensive ever undertaken on the fishery and covered the three major habitats in which the fishery operates; river (estuarine), intertidal (0 – 2 m depth) and inshore coastal (2 – 25 m depth). At least 38 species of elasmobranchs were found to occur within the fishery, however the catch was dominated by Carcharhiniformes; 95% of individuals were from 25 species of the families Carcharhinidae, Hemigaleidae and Sphyrnidae. The main carcharhiniform taxa could be qualitatively categorised into four groups based on similar catch characteristics and life history traits: small coastal species (<1000 mm) were captured primarily as adults, moderate sized coastal species (1000–2000 mm) were captured at all sizes, large coastal semi-pelagic species (>2000 mm) were captured primarily as neonates or juveniles, and hammerheads were captured at all sizes.

The life history characteristics of five species occurring in the fishery were investigated in detail using biological samples collected during the observer program, from fishery-independent

sampling, and from purchase or donation from commercial fishers. The milk shark, *Rhizoprionodon acutus* was the fourth largest component of the elasmobranch catch by number in the ECIFF, making up 7.8 % of all carcharhiniform sharks caught. Growth was rapid in this species; von Bertalanffy growth parameters for males were $L_{\infty} = 821$ mm, $k = 0.94$ and $L_0 = 424$ mm and for females were $L_{\infty} = 859$ mm, $k = 0.63$ and $L_0 = 423$ mm. Females and males attained a maximum age of 8.1 and 4.5 years, respectively. The size at which 50% of females and males were mature was 780 and 742 mm, respectively. The age at which 50% of females and males were mature was 1.8 and 1.1 years of age, respectively. Despite being widely distributed globally and heavily exploited throughout its range, these are the first comprehensive estimates of age, growth and maturity for this species.

The life histories of two globally endangered hammerhead sharks captured by the ECIFF were also examined in detail. The scalloped hammerhead, *Sphyrna lewini* and the great hammerhead, *S. mokarran*, were the fourth and third largest components of the elasmobranch catch by weight in the ECIFF. The catch of *S. lewini* was heavily biased towards males and significant differences in growth and maturity characteristics were found between those occurring within the GBRWHA and individuals sampled from temperate waters off northern New South Wales. The life history of females was difficult to establish as adults could not be sourced from any fishery. The best-fit estimates for a three-parameter von Bertalanffy growth curve fit to both sexes were $L_{\infty} = 3312$ mm, $L_0 = 584$ mm and $k = 0.076$. Males attained a maximum age of at least 21 years while the longevity of females could not be determined. For *S. mokarran*, the best-fit growth parameters for a two parameter von Bertalanffy growth curve fit to both sexes and assuming a fixed size at birth (L_0) of 700 mm, were $L_{\infty} = 4027$ mm, and $k = 0.079$. Females lived to at least 39.1 years and males to at least 31.7 years. Length and age at 50% maturity was not significantly different between sexes and occurred at 2279 mm and 8.3 years.

The spot-tail shark, *C. sorrah*, is the second most important component of the elasmobranch catch in the ECIFF both by number and weight. For *C. sorrah* the best-fit growth parameters for a two parameter von Bertalanffy growth function with a fixed length at birth (L_0) of 550 mm were $L_{\infty} = 1085$ mm, and $k = 0.5513$ for males and $L_{\infty} = 1265$ mm, and $k = 0.3389$ for females. Growth was not sexually dimorphic prior to reaching maturity and as such 50% maturity occurred at 933 mm and 2.3 years in both sexes. Fifty percent maternity occurred at 1029 mm and 3.4 years indicating females began reproducing 1–2 years after reaching maturity. Males attained a maximum age of at least 9 years and females at least 14 years. Females had an annual, synchronous reproductive

cycle with ovulation occurring in March and parturition in early December after a gestation period of approximately 9 months. Females gave birth to between 1 and 6 pups of approximately 550 mm in length, and there was an increasing relationship between maternal length and fecundity.

The largest component of the elasmobranch catch in the ECIFF was the Australian blacktip shark, *C. tilstoni*. However, analysis of the life history of this species was confounded by the presence of the morphologically similar common blacktip shark, *C. limbatus*. Genetic methods were used to distinguish between these species, however a mismatch was found between identification using genetics and identification by vertebral counts. This mismatch was thought to be due to hybridisation between the two species. As there was no clear way to distinguish between the two species, a multi-faceted approach to species identification was developed.

Following this, best fit growth parameters for *C. tilstoni* using a two parameter von Bertalanffy growth function with a fixed length at birth (L_0) of 619 mm were $L_\infty = 1748$ mm, and $k = 0.137$ for males and $L_\infty = 2138$ mm, and $k = 0.099$ for females. However, growth was more accurately described by a two-phase variant of the von Bertalanffy growth function that suggested a cessation in growth occurs around 4.1–4.5 years of age. Like *C. sorrah*, growth was not sexually dimorphic prior to maturity and 50% maturity occurred at 1208 mm and 5.5 years in both sexes. Fifty percent maternity occurred at 1374 mm and 7.5 years indicating that females began reproducing approximately 2 years after maturity. *Carcharhinus tilstoni* has an annual, synchronous reproductive cycle, with ovulation occurring in March and parturition in early December after a gestation period of approximately 9 months. Females gave birth to between 1 and 7 pups with a mean size at birth of 621 mm.

The carcharhiniform sharks captured by the Queensland ECIFF display a range of life history characteristics ranging from small (<1000 mm) and rapidly growing ($k = 0.94$) species such as *R. acutus* to large (>4000 mm) and slow growing ($k = 0.079$) species such as *S. mokarran*. An appreciation of these life history characteristics is essential in data deficient fisheries such as the ECIFF where the productivity of captured species differs greatly and some species may be more vulnerable to overexploitation than others. This highlights the importance of ongoing studies on life history of sharks. The new life history data from the research should be used to help improve the management of the ECIFF and can help provide a sounder biological basis for decision making.

Chapter 1. General Introduction



Plate 1. Dawn in Bowling Green Bay (April 2009).

1.1 INTRODUCTION

Humans have utilised sharks for thousands of years, both in modern and ancient civilisations, for a variety of purposes including for their flesh, oil and leather, and for medicinal purposes (Walker, 1998). Sharks belong to the class Chondrichthyes, a group of fishes that has existed for at least 400 million years and that has evolved to exploit almost all aquatic habitats and niches (Compagno, 1990a). In spite of their evolutionary success, chondrichthyans have coped poorly with the explosion of anthropogenic influences that has accompanied the progressive and ongoing industrialisation of humanity since the nineteenth century. Undoubtedly the single biggest anthropogenic influence on shark populations has been the expansion of commercial fishing (Bonfil, 1994).

The contribution of cartilaginous fishes, including sharks, to commercial fisheries is small relative to teleosts — they have traditionally made up around 1% of global fisheries production (Compagno, 1990b). Yet, the historical success of shark fisheries has been poor. Many are typified by a rapid expansion or ‘boom’, followed by an equally rapid ‘bust’, when initially high catch rates drop and the fishery becomes uneconomical. For example, demand for liver oil after World War II led to overfishing of school shark, *Galeorhinus galeus* throughout much of its range (Ripley, 1946; Olsen, 1959). Commercial fishing of basking sharks, *Cetorhinus maximus*, rapidly depleted populations of this species in parts of the world (Parker and Stott, 1965). Since the mid 1990s, reports of declining shark stocks have taken a more worrying form. Occasional reports of single-species collapses have now been replaced by meta-analyses reporting declines across entire assemblages of predatory fish (Pauly *et al.*, 1998; Christensen *et al.*, 2003; Morato *et al.*, 2006). For example, Ferretti *et al.* (2008) reported on the removal of large sharks in the Mediterranean caused by a long history of fishing. Severe declines in large sharks have also been reported in the northwest Atlantic and Gulf of Mexico (Baum *et al.*, 2003; Baum and Myers, 2004), although there is debate on the magnitude of these declines (Burgess *et al.*, 2005).

It is now well-recognised that the life history traits of sharks and other chondrichthyans make them more susceptible to overfishing than many teleosts (Stevens, 1999b). Shark life histories are often typified by large body sizes, slow growth rates, low fecundity and low rates of natural mortality (Cortés, 2004). Hence, shark fisheries managed using methods devised for teleosts have often failed (Holden, 1974). A larger problem, though, has been the widespread absence of

management among fisheries targeting and interacting with sharks. Holden (1974) is often credited as first recognising many of the issues relating to exploitation of sharks and offered some early solutions. Despite Holden's work, the first concerted global push for shark research did not come about until the 1980s. A report compiled by the United States National Oceanic and Atmospheric Administration summarised much of the collective knowledge at the time (Pratt *et al.*, 1990). This also coincided with the first widespread recognition of the conservation issues facing sharks globally (Manire and Gruber, 1990).

Fisheries research on sharks has progressed considerably since the 1980s, although it still lags well behind that of teleosts. Standard protocols for research have been developed in critical fields such as age and growth (Cailliet, 1990; Cailliet and Goldman, 2004; Cailliet *et al.*, 2006), and reproductive biology (Walker, 2005b). Alternatives to traditional stock assessment methods have also advanced considerably in the past two decades, especially the modelling of population dynamics (Cailliet, 1992; Cortés, 2004; 2007). Yet, unlike teleosts, there are few long-term monitoring programs dedicated to the collection of biological material such as gonads and vertebrae from sharks. As such, life history information itself remains fragmentary for many species. For example, the length of the reproductive cycle of the blue shark, *Prionace glauca* remains unknown (Aires-da-Silva and Gallucci, 2007), despite it being perhaps the most abundant and heavily exploited of all sharks globally. While growth rates have been reported in many species, these have only been validated in a handful of cases, and most growth studies still rely on indirect methods for verifying the age of individuals (Cailliet *et al.*, 2006). Consequently, there is a critical need for studies into the life history to help predict how sharks may be affected by fisheries.

In Australia, commercial fishing of sharks for their flesh is well-established, especially in the southern states where shark flesh is marketed as 'flake'. However, Australia differs from many other nations in that research and management have accompanied the development of several of its shark fisheries (Olsen, 1959; Simpfendorfer and Donohue, 1998). As a direct result of this, some of the few examples of sustainable shark fisheries occur in Australian waters (Walker, 1998). Despite this, Australian shark populations have by no means been immune to overexploitation (Stevens and Davenport, 1991; Punt and Walker, 1998; Graham *et al.*, 2001; Otway *et al.*, 2004), and the strong history of research and management has not extended to all fisheries. Reflecting the lower demand and value of shark products from tropical northern Australia, the fisheries interacting with sharks in these areas are among the least well studied.

Current management of Australia's northern shark resources is based principally on a research project carried out during the 1980s (Stevens and Davenport, 1991). That study the first and only major study of its kind in northern Australia was driven by Australian interest in developing a commercial fishery for sharks and by concerns of overfishing from a large-scale Taiwanese fishery operating in the area at the time (Walter, 1981; Stevens and Wiley, 1986). When tighter restrictions and declining catch rates forced the closure of the Taiwanese fishery in 1986, it resulted in the end of large-scale commercial fishing for sharks across northern Australia. Coincident with this was a large reduction in fisheries research. But while large-scale commercial fishing ended in 1986, a number of small-scale domestic fisheries have continued to exploit sharks across northern Australia (Bensley *et al.*, 2010). In recent years, as the value of shark fin has increased, there has not only been an increase in domestic fishing (Gribble *et al.*, 2005), but also an increase in illegal, unreported and unregulated fishing across northern Australia by neighbouring countries (Field *et al.*, 2009; Marshall, 2011). Hence, there is once again a critical need for collection of data to help inform management of sharks across northern Australia.

One particularly data deficient region of northern Australia is the northeast coast of Queensland. With the exception of a small number of research projects on individual species (e.g. Simpfendorfer, 1992a; Simpfendorfer, 1993; Robbins, 2006), there has been little study of elasmobranchs here. This lack of research is surprising given that the region includes Queensland's largest extractive fishery for sharks, the East Coast Inshore Finfish Fishery (ECIFF), and the Great Barrier Reef World Heritage Area. Historical monitoring of the shark catch in the ECIFF has been minimal (Rose *et al.*, 2003) and previous research across northern Australia may not be applicable to the east coast of Queensland as it was mainly conducted in the Arafura Sea (Stevens and Davenport, 1991).

1.2 PROJECT STRUCTURE AND OBJECTIVES

Reflecting the need for more information to effectively manage northern Australia's shark populations, research projects involving sharks have been given high priority since the mid 2000s, especially in hitherto unstudied regions such as the Great Barrier Reef World Heritage Area (GBRWHA). This PhD study was a component of two, inter-related, and federally funded research projects. The largest of these was Marine and Tropical Scientific Research Facility (MTRSF) Project 4.8.4, entitled "*Evaluation of the impacts from industry and community uses on*

inshore biodiversity” which ran from July 2006 to June 2010. Two objectives of this project were to:

“Derive biological parameters, determine stock structure and identify critical habitats for key inshore species, particularly sharks, used by industry and community” and,

“Evaluate the impacts of industry and community use on key inshore marine species, such as sharks, within the GBRWHA by identifying vulnerable species or species groups and assessing potential risks.”

This PhD study was also a component of Fisheries Research and Development Corporation Project 2007/035, the aims of which were:

“To determine the spatial and temporal stock structure of fished shark species along the east coast of Queensland” and,

“To use stock structure information to define appropriate management units for sustainable management of shark resources along the Queensland east coast.”

The above projects provided research funding and a partial stipend for this PhD study, and also helped dictate its objectives and timeline. The over-arching objective of this study was therefore to provide information that could be used to assist in the management of commercially fished sharks in Queensland in general, but specifically within the Great Barrier Reef World Heritage Area. Research of this nature is timely given the current global crisis in biodiversity (Jackson *et al.*, 2001), which has the potential to adversely affect sharks (Stevens *et al.*, 2000a; Dulvy *et al.*, 2008). It is also timely given that many of the focal species of this PhD study have been commercially harvested within the Great Barrier Reef World Heritage Area for several decades with little documented knowledge of the catch levels or potential effects of fishing.

Much of the content presented here draws and expands on work undertaken by John Stevens and colleagues that was carried out across northern Australia during the 1980s (Stevens and Davenport, 1991). Until now, that research has been the only reference for basic life history data for a number of species, both in Australia and other parts of the world. Long-term, tag-return data

from that study also provides some of the only records of maximum longevity for tropical sharks. This PhD study aims to build on this previous work carried out in the Arafura Sea, especially by expanding on the number of species for which there are age and growth data available.

1.3 SOURCE OF DATA

Biological samples for this research were principally obtained from an onboard vessel observer survey program undertaken as part of MTSRF Project 4.8.4, in which the author was one of three main observers collecting data. Additional samples were obtained via fishery-independent sampling undertaken in collaboration with several postgraduate student research projects, in which the author participated. Further samples were obtained through direct purchase or donation from fishermen, and through collaboration with research and management organisations in Queensland and New South Wales.

1.4 THESIS OUTLINE

- **Chapter 2** provides a summary of the onboard vessel observer survey program undertaken during MTSRF Project 4.8.4, from which the majority of samples for this thesis were sourced. This chapter provides the first detailed information on the catch composition of sharks from the ECIFF within the GBRHWA and discusses some of the issues faced by this and similar small-scale shark fisheries worldwide.
- **Chapter 3** of this thesis examines, for the first time, age, growth and maturity of the milk shark, *Rhizoprionodon acutus*, a species of high commercial importance throughout the tropics worldwide. The reproductive mode of this species meant that traditional age and growth methods were unable to provide accurate results, so a novel method is described to account for this.
- **Chapter 4** describes the biology of two globally endangered hammerhead species that are caught by the ECIFF. Successful validation of growth in the great hammerhead, *Sphyrna mokarran*, was enabled through a mark, tag and recapture study. Intraspecific differences in the biology of male *S. lewini* are discussed.
- **Chapter 5** addresses the age-old question of what it means to be a species. Two established methods for distinguishing between cryptic blacktip species are examined and compared, with conflicting results. A protocol to distinguish between the two species is provided as an appendix.

- **Chapter 6** provides a quantitative analysis of age, growth, maturity, maternity and reproductive biology for use in management of the two most commercially important sharks caught from tropical northern Australia: the Australian blacktip shark, *Carcharhinus tilstoni* and the spot-tail shark, *Carcharhinus sorrah*.
- **Chapter 7** provides a practical application of the life history data collected in Chapter 4 to construct a population model for the scalloped hammerhead, *S. lewini*. Catch of this species was strongly biased toward males in the GBRHWA. The potential effects, both positive and negative, of male-biased harvesting are examined using demographic models. The implications of sex-biased harvesting on other large sharks are also explored.
- **Chapter 8** concludes the thesis by discussing the fishery implications of this research. A summary of the life-history data now available for Queensland's commercially harvested inshore sharks is provided and remaining knowledge gaps and research priorities are identified.

The intention of this thesis is to publish all chapters containing new data (2–7). Three chapters published at the time of submission are included in this thesis verbatim. Digital Object Identifiers are provided for those chapters so that they may be viewed in a more reader-friendly format.

Chapter 2. Evaluating catch and mitigating risk in a multi-species, tropical, inshore shark fishery within the GBRWHA



Plate 2. Juvenile spinner sharks, *Carcharhinus brevipinna*, caught by a commercial net boat off Rattlesnake Island (September 2010)

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2.1 INTRODUCTION

Ongoing worldwide fisheries exploitation continues to fuel a growing debate on the future of wild-caught fisheries (Jackson, 2008; Worm *et al.*, 2009). Higher trophic-level predators such as elasmobranchs (sharks and rays) have fared particularly poorly, with some often rapid collapses of populations where they are targeted or taken as by-catch (Ripley, 1946; Olsen, 1959; Graham *et al.*, 2001; Devine *et al.*, 2006). Recently, international concern over the ongoing exploitation of sharks has led to the development of the International Plan of Action for Sharks (FAO, 2000). The vulnerability of sharks and rays to overfishing stems largely from their life history characteristics, including late maturation, low fecundity, low natural mortality, and long life-spans (Cortés, 2000). These characteristics mean there is a close relationship between stock size and recruitment, and consequently long recovery times after overexploitation has occurred (Holden, 1974).

Other factors such as naturally low abundance as well as complex migration patterns and spatial usage (e.g. sex segregation, site fidelity (Heupel and Simpfendorfer, 2005; Sims, 2005)) can further increase the vulnerability of some elasmobranchs to overfishing. This is relevant to carcharhiniform sharks, particularly of the families Carcharhinidae and Sphyrnidae, which occur abundantly throughout inshore continental shelf regions of the tropics and subtropics worldwide (Musick *et al.*, 2004).

Species of these families vary greatly both in their life histories and their utilisation of inshore habitats (Knip *et al.*, 2010). For example, many small to medium sized carcharhinids (e.g. *Rhizoprionodon taylori*, *Carcharhinus sorrah*) remain within inshore areas throughout the duration of their lives. These species are often fast growing and relatively short lived (Davenport and Stevens, 1988; Simpfendorfer, 1993). Other carcharhiniform sharks utilise inshore habitats only during discrete stages of their lives. These species are generally larger in size and have moderate to slow growth rates; *Negaprion brevirostris* and *C. leucas* are examples of species that use inshore areas as neonate and juvenile nurseries (Springer, 1950; Castro, 1993). Conversely, neonates of other species (e.g. *Galeocerdo cuvier*, *Sphyrna mokarran*) are absent from close inshore waters whereas adults are present (Hueter and Tyminski, 2007). The wide variety of life history characteristics and space utilisation means inshore shark populations are likely to be

affected in a range of different ways and to varying extent by anthropogenic influences such as fishing.

Artisanal and commercial fisheries for carcharhiniform sharks exist in most equatorial and tropical regions and are particularly common throughout Asia, especially in the Indo-Pacific region and the Indian subcontinent (Kasim, 1991; Hanfee, 1999; Henderson *et al.*, 2007; White, 2007), as well as parts of Africa, the Caribbean, and throughout Central America (Motta *et al.*, 2005), notably Mexico (Castillo-Geniz *et al.*, 1998). Despite the important contribution these fisheries make to regional economies and food security, management of such fisheries is often neglected (Fowler *et al.*, 2005). Many countries lack the resources to adequately monitor their fisheries (White and Kyne, 2010), and even in more affluent states the inherent low value of inshore shark fisheries often mean research and management are given low priority. Where monitoring is conducted, catch composition is rarely established because of the difficulties in identifying many species so, at best, sharks are identified only to family or order (Shotton, 1999). The paucity of data on most inshore tropical shark fisheries along with wide variation among life histories and complex spatial ecology provides an imposing hurdle to sustainable harvest of carcharhiniform sharks in these fisheries and raises concerns given the vulnerability of elasmobranchs to overfishing.

In tropical northern Australia, carcharhiniform sharks make up large components of several small-scale, inshore fisheries targeting a range of teleost and shark species (Stevens, 1999a; Salini *et al.*, 2007). The low value of tropical shark (\$2–3AU kg⁻¹ processed weight) means that despite Australia's status as a developed nation, many of these fisheries are similar to those in developing nations: fishing effort is highly fragmented along the coastline, fishing vessels are usually small in size (< 7 m), and nets are frequently hauled by hand. Aside from the period between 1974 and 1986 when Taiwanese gill-net vessels targeted sharks off northern Australia, the total harvest of elasmobranchs in Australia's tropical fisheries has been between 2000 – 3000 tonnes yr⁻¹ (Bensley *et al.*, 2010). While some components of northern Australian shark fisheries have been reasonably well monitored and formal risk assessments or stock assessments used to inform management, other areas, including the east coast of Queensland have received little attention (Anon, 1990; Stobutzki *et al.*, 2002; Salini *et al.*, 2007). This is somewhat surprising given that on the east coast of Queensland these fisheries occur within the Great Barrier Reef World Heritage Area (GBRWHA), one of the world's largest networks of marine protected areas (GBRMPA, 2009).

Changes to legislative requirements concerning sustainability in Australian fisheries (*Environmental Protection and Biodiversity Conservation Act 1999*), combined with a 200% increase in shark landings on Queensland's east coast between 1993 and 2004 (Bensley *et al.*, 2010) and concern from managers about shark exploitation within the GBRWHA (GBRMPA, 2009) recently created a need to describe the shark component of the inshore net fishery. Consequently, between 2006 and 2009 an onboard-vessel observer study recorded the catch composition and harvest practices of the fishery. The aims of this study were to quantify the composition, to species level, of carcharhiniform sharks caught by net fisheries in the GBRWHA and to examine the characteristics of the catch to qualitatively establish patterns of catch susceptibility. To this end we compared catch rates between three nominal zones (rivers, intertidal and inshore coastal), examined the sex ratio of the catch and compared male and female length frequency distributions. We discuss emergent patterns in the catch in relation to life history characteristics and consider the threats to carcharhiniform sharks in the GBRWHA. Given these new data we also suggest fisheries management strategies aimed at mitigating the risk of overfishing, and we consider the implications for management in data-poor, inshore fisheries for carcharhiniform sharks throughout tropical regions of the world.

2.2 METHODS

2.2.1 Fishery observer program

Between June 2006 and July 2009, fishery observers monitored vessels operating in the commercial gillnet sector of the Queensland East Coast Inshore Finfish Fishery (ECIFF) within the boundaries of the GBRWHA which are between Cape York (10.5°S) and Bundaberg (24.5°S) (Figure 2.1). The vast area of the fishery meant data were collected simultaneously by two groups, James Cook University Fishing & Fisheries Research Centre and Fisheries Queensland. Data were subsequently combined to provide the most robust dataset. Fisher participation in the observer survey was voluntary. Prior to commencing a trip, the observer interviewed the fisher to determine the length, depth, and mesh size of net to be used, so fishing effort could be calculated. Fishing start time for an individual net shot was recorded as the time when the net was completely in the water, and finish time was when hauling of the net began. Location of nets was recorded using a hand-held GPS and depth was measured using an onboard depth-sounder. Catch composition of elasmobranchs was recorded to species level using a species identification key

derived from Last and Stevens (1994). Owing to the small-scale nature of the fishery, a single observer assessed each individual trip. When conditions permitted, the stretch-total length, fork length and pre-caudal length (sharks) or disc width (rays) of a sub-sample of the catch was recorded in mm (Compagno, 1984) and weight measured in kg. When possible, sex and maturity stage of sharks processed at sea was also recorded using a standard staging system (Walker, 2005b).

2.2.2 Fishery zones

Data were grouped into three broad zones (river, intertidal, and inshore coastal) that corresponded to discrete sub-components of the ECIFF, each with different resident species, targeting and harvest practices, and management strategies (Table 2.1). In river zones barramundi, *Lates calcarifer*, was targeted using set nets with stretched mesh sizes of 165–216 mm. Nets were usually set overnight and fishing occurred between February and October. Within intertidal zones (defined as waters < 2m depth) several teleost species (mostly *Eleutheronema tetradactylum*, *Polydactylus macrochir* and species of the family Mugilidae) were targeted using set nets with stretched mesh sizes of 114–216 mm. Fishing in intertidal zones occurred throughout all periods of the day and throughout the year. Within inshore coastal zones (defined as coastal waters of between 2 and 25m depth) *Scomberomorus semifasciatus* were targeted during winter and spring, while a generalist shark fishery targeting mainly *Carcharhinus tilstoni* and *C. sorrah* operated throughout the year. Some fishers were licensed to use up to 1200 m of 165 mm stretched mesh net, although most were licensed to use 600 m.

2.2.3 Data analysis

Some of the earlier Fisheries Queensland observer trips were primarily focused on recording teleost catch, so identification of Carcharhinidae and Sphyrnidae species was limited to family level (e.g. “whaler shark”). With the exception of overall catch composition (Table 2.3), these trips were excluded from further analyses, which focused only on carcharhiniform sharks. Mean length at capture was calculated and, although not all animals were measured, the recorded lengths were assumed to represent a random sub-sample of the total catch. Mean weight at capture was calculated using length-weight regressions derived from the present study or, if unavailable, from previous studies in northern Australia (Stevens and Lyle, 1989; Stevens and McLoughlin, 1991). Catch was standardised to number per unit effort (individuals km-net-hour⁻¹) and weight per unit effort (kilograms km-net-hour⁻¹). To further examine characteristics of the

overall catch (data pooled between zones), two-sample Kolmogorov-Smirnov tests were used to test whether length-frequency distributions of males and females of individual species were significantly different. The sex ratio (females/males) of the catch was also calculated and, where there were at least 5 individuals from each sex, Chi-squared tests used to determine any significant differences in sex ratio. All of the Carcharhiniformes caught in the present study had a reproductive mode of placental viviparity (except for the tiger shark, *Galeocerdo cuvier*), so the percentage of neonates in the catch could be inferred from the presence of an open or unhealed umbilical scar, thus indicating recent birth. The catch characteristics above were used to qualitatively establish the susceptibility of different species to the fishery. Capture susceptibility was defined as the culmination of factors that result in an individual of a species being killed by the fishery (e.g. availability, encounterability, selectivity (Walker, 2005b)). We considered susceptibility in the general sense of the term and no attempt was made to quantify it, e.g. Stobutzki *et al.* (2002). Emergent patterns in the catch were further discussed in relation to the life history characteristics of captured species such as length at 50% maturity, growth characteristics, and habitat preferences. Life history data was obtained from the published literature or, if available, from unpublished data obtained during the present study.

2.3 RESULTS

2.3.1 Fishery observer survey

Between June 2006 and July 2009, observers were deployed on 149 often multi-day fishing trips within the GBRWHA. Observations were on 1188 separate net shots during 297 days onboard vessels giving a total of 1452 km net hours (Table 2.2).

2.3.2 Spatial distribution of fishing effort

Although 60% of trips occurred in intertidal zones, the greatest amount of fishing effort was observed in inshore coastal zones (Table 2.2). This reflected the generally shorter duration of trips occurring in intertidal and river zones ($\bar{x} = 1.3$ days, and $\bar{x} = 2.4$ days, respectively), compared with those in inshore coastal zones ($\bar{x} = 3.5$ days), and also the generally shorter net lengths used in intertidal and river zones. The longest trip observed in all zones was seven days, while the shortest was < 1 day (i.e. a single-day trip). Total effort observed was 202 km-net-hours in river

zones, 237 km-net-hours in intertidal zones and 1013 km-net-hours in inshore coastal zones (Table 2). All observed fishing effort was between 13°S and 24°S (Figure 2.1).

2.3.3 Catch composition

A total of 18,625 fish were recorded by observers including 6,828 elasmobranchs that constituted 37% of the catch by number. Overall, 38 species of elasmobranchs from 11 families and 4 orders were identified (Table 2.3) of which Carcharhiniformes was both the most diverse order (25 species) and the largest component of the catch by number (94.5%). The Rajiformes was the next most diverse order (> 10 species) but only contributed 3.9% of the elasmobranch catch by number. The remaining 1.6% came from two species of Pristiformes, three species of Orectolobiformes and a small number of unidentified sharks. After the removal of trips that contained fish identified only to family level, species-level catch composition was determined for 126 trips with a total effort of 905 km net hours. Among the Carcharhiniformes (Table 2.4), the morphologically identical blacktip sharks, *C. tilstoni* and *C. limbatus* were the most numerous (28%, Table 2.4). These species could not be separately identified in the field and were therefore grouped together. Spot-tail shark, *C. sorrah*, and scalloped hammerhead, *S. lewini*, were also relatively large contributors to the catch number (17% and 11%, respectively Table 2.4). By weight, the target species of the fishery, *C. tilstoni/C. limbatus* and *C. sorrah* also dominated the catch, contributing ~51% of the catch (Table 2.4). Despite being only 2.4% of the catch by number the great hammerhead shark, *Sphyrna mokarran*, was the third largest component of the total weight (9.64%), due to its large mean size at capture (Table 2.4). Conversely, catch by weight of some smaller species (e.g. *R. acutus*, *R. taylori*) as a proportion of total catch was lower than their respective proportion of catch by number.

Diversity of carcharhiniform sharks captured increased with distance from the coast, with 7 species recorded in rivers, 17 species in intertidal zones, and 25 species recorded in inshore coastal zones (Table 2.3). Number and weight per unit effort of Carcharhiniformes also increased with distance from the coast caught (Table 2.4). Compared with river zones, the catch of Carcharhiniformes was approximately 5 times greater in intertidal zones, and 9 times greater in inshore coastal zones. *Carcharhinus tilstoni/C. limbatus* were by far the most captured species in both the intertidal and inshore coastal zones, and also accounted for the greatest weight. *Carcharhinus sorrah* accounted for a large component of the catch in inshore coastal zones, although was rarely caught in intertidal zones. Although few were caught, the large size of *S.*

mokarran meant it accounted for a relatively large component of weight in both intertidal and inshore coastal zones. *Carcharhinus leucas* was the only species regularly captured in river zones.

2.3.4 Catch characteristics

Mean lengths of species within the overall catch (all zones pooled) ranged from 637 mm for male *R. taylori* to 1544 mm for female *S. mokarran* (Table 2.5, Figure 2.2). Sex-specific differences in the length-frequency distributions were found for six of the 14 species where there were sufficient data to carry out the KS test (Table 2.5). A significant difference in the sex ratio of the catch was also found for six of the 14 species tested (Table 2.5). No clear trends in sex ratio were evident, with females greatly outnumbering males in some species such as *S. mokarran* and *R. taylori*, and males greatly outnumbering females in other species such as *S. lewini* and *R. acutus*. There was also considerable interspecific variation in the different life stages present within the catch (Table 2.5). Percentages of neonates recorded in the catch ranged from 0% for many species up to 62.1% for the bull shark, *Carcharhinus leucas*. The percentages of mature animals in the catch was inversely related to maximum size for many species, as small species (< 1000 mm) were typically caught as adults, and moderate to large species (> 1000 mm) were caught as juveniles. Exceptions to this trend included the snaggleteeth shark, *Hemipristis elongata* and the winghead shark, *Eusphyra blochii* that were both moderate sized species (up to 2000 mm) mainly caught as adults. Large sex-specific differences were also found in the percentage of the catch mature for some species, including *R. acutus* and *S. lewini* where adult males were present in the catch, but adult females were either rare or absent. For the blacktip complex of *C. tilstoni*/*C. limbatus*, the percentage of mature animals should be considered an approximation, as it was based on length at maturity of *C. tilstoni* and likely included some *C. limbatus*. Off eastern Australia, *C. limbatus* is known to mature at sizes > 2000 mm (Macbeth *et al.*, 2009), which is larger than any individuals measured during the observer survey. Therefore although an accurate estimate of the percentage of mature *C. tilstoni* was not possible, we have a high level of confidence that no adult *C. limbatus* were caught.

2.4 DISCUSSION

2.4.1 Capture susceptibility and threats to carcharhiniform sharks in the GBRWHA

The present survey of the mesh-net commercial fishery operating within the GBRWHA revealed the complex nature of tropical shark fisheries. At least 38 species of elasmobranchs were recorded in the catch, with catch rates varying between habitats, life stages (neonate, juvenile, adult) and by sex. Despite this complexity, some broad trends in capture susceptibility were seen among the Carcharhiniformes (Table 2.6). For example, small species < 1000 mm in total length (e.g. *R. acutus*, *R. taylori*) were, by virtue of their small size relative to the net mesh size, almost exclusively susceptible to capture as adults in the fishery. Moderate sized species 1000–2000 mm total length (e.g. *C. tilstoni*, *C. sorrah*) were susceptible to some extent at all sizes with neonates large enough and young adults small enough to be caught by the nets. In contrast, large species > 2000 mm total length (e.g. *C. amboinensis*, *C. brevipinna*) were subject to a gauntlet effect, whereby only a small number of juveniles age classes caught by the fishery (Simpfendorfer, 1999; Prince, 2005). Large species were frequently captured as neonates and juveniles and rarely caught as adults possibly due to adults migrating away from fished habitats or growing too large to be meshed or entangled by the nets. Hammerhead sharks typified another group of species susceptible in similar ways. Despite growing to a large size they were susceptible to capture at all sizes due to their head morphology.

The results of this study confirm that carcharhiniformes dominate the catch of the ECIFF and it is elasmobranchs of this order that are probably most at risk from the fishery. Many of the species caught by the ECIFF were also identified by risk assessments as among the least likely to be sustainable across other northern Australia fisheries (Stobutzki *et al.*, 2002; Salini *et al.*, 2007) and are also probably affected to some extent by recreational fishing within the GBRWHA (Lynch *et al.*, 2010). Stocks of some species are known to be shared with other nearby jurisdictions so unsustainable fishing practices in these areas would also potentially affect GBRWHA populations (Ovenden *et al.*, 2009), as would illegal fishing encroaching on northern Australian waters (Field *et al.*, 2009). In contrast to the threats posed by fishing, an integrated risk assessment for climate change of the GBRWHA suggested that most of the Carcharhiniformes caught in the ECIFF were unlikely to have a high vulnerability to climate change due to their high adaptive capacities (Chin *et al.*, 2010).

Of the non-Carcharhiniformes, most were caught in relatively low numbers with the exception of cownose rays, *Rhinoptera* spp., narrow sawfish, *Anoxypristis cuspidata*, and wedgefish, *Rhynchobatus* spp., all of which were at least 1% of the overall catch by number. The record of seven green sawfish, *Pristis zijsron*, in the catch indicates this species is still present on the east coast of Queensland at least as far south as the Whitsundays (20°S) even though it is now considered to be extinct in New South Wales waters (Fisheries Management Act 1994, NSW, No. 38). Recent protection of sawfish in Australian waters as well as catch restrictions imposed on wedgefish in the ECIFF are likely to partially mitigate the threats posed to at least two of the families listed above.

2.4.2 Risk mitigation strategies in multi-species, tropical shark fisheries

The diversity of elasmobranchs within the tropical coastal regions of the world, combined with the complex spatial ecology and behaviour patterns they exhibit clearly provides a major challenge for sustainable management of extractive fishing. It has long been recognised that the idiosyncrasies of shark populations and fisheries require alternative approaches to management compared with teleost resources (Holden, 1974). More recently it has also been shown that the features of elasmobranchs that make them vulnerable (e.g. close stock-recruitment relationships) can also be advantageous when properly managed (Walker, 1998). Indeed, the idiosyncrasies of shark populations may provide many under-utilised opportunities for designing management strategies, and if properly understood may help reconcile some of the impediments to sustainable management.

Perhaps one of the simplest observations that can be taken from the present study is that despite the large number of species caught within the ECIFF, there were only several patterns in the way they were susceptible (Table 2.6). In many instances, similarly susceptible species also shared similar life history traits. For example, many small, coastal tropical carcharhiniform sharks (< 1000 mm, e.g. *R. acutus*, *R. taylori*) are amongst the fastest growing and most productive of elasmobranchs so far studied (Simpfendorfer, 1993) (Chapter 3). Medium sized (1000–2000 mm, e.g. *C. cautus*, *C. sorrah*, *C. tilstoni*) coastal tropical species are somewhat less productive, typically living 10–20 years and maturing relatively young (Davenport and Stevens, 1988; White *et al.*, 2002). In contrast, large tropical Carcharhiniformes (> 2000 mm e.g. *C. leucas*, *N. brevirostris*) typically conform to the slow-growing, long-lived paradigm more frequently associated with elasmobranchs (Brown and Gruber, 1988; Neer *et al.*, 2005). These similarities

also extend to habitat and spatial usage. Most species within the small and medium sized groups are restricted to coastal waters, while in comparison most large species are semi-pelagic, migrating offshore at larger sizes.

These life history patterns have been recognised and described by a variety of authors in the past (Hoenig and Gruber, 1990; Cortés, 2000; Frisk *et al.*, 2001). While actual groupings themselves are arbitrary (e.g. small, medium, large), the underlying concept of a life history continuum, ranging from ‘slow’ to ‘fast’ species (Cortés, 2002), has important implications in terms of simplifying management of multi-species fisheries. Although species-specific management may be unfeasible, it may be possible to direct management strategies at species that are not only susceptible in the same way, but also have similar life history traits (e.g. the management of ‘Small Coastal Shark’ and ‘Large Coastal Shark’ complexes in the United States). In the case of the ECIFF, management of the fishery could potentially be simplified by directing management strategies at the four nominal groups identified in Table 2.6.

Examples of specific management strategies which could be used to mitigate the risk of overfishing to tropical carcharhiniform sharks may involve the use of gear restrictions and spatial and temporal closures. Modifying the gear selectivity in a fishery to take advantage of particular life history traits may be one of the most effective measures for mitigating risk. This is especially relevant in gillnet fisheries for sharks where size-selectivity dynamics are well understood compared to other gear types such as trawl and line (Kirkwood and Walker, 1986). In the present study the exclusive use of small-mesh gillnets (typically < 165 mm) by the ECIFF meant sharks > 1500 mm were rarely captured (with the exception of hammerheads). This in itself may be a good strategy for multi-species tropical shark fisheries, as only neonates and juveniles of the largest (and often least productive) species are captured by the fishery, while adults are subject to a ‘gauntlet’ effect and effectively excluded. The concept of the gauntlet fishery has been proposed as an effective method of harvesting long-lived species, providing that fishing mortality on adults remains extremely low (Simpfendorfer, 1999; Prince, 2005). Although such a harvest strategy is unlikely to provide the maximum sustainable yield (Gallucci *et al.*, 2006), it may be preferable depending on the goals of the fishery. In an artisanal fishery, for example, the harvest of large sharks is unlikely to contribute to food security given that the flesh from these animals often contains high levels of mercury and may not be suitable for human consumption (Lyle, 1984; Clarkson, 1997). In the case of the ECIFF, the use of a gauntlet style-harvest strategy potentially provides a lower-risk method of harvesting the large coastal/semi pelagic species, but at the same

time allows for concurrent harvest of the more productive small and medium coastal sharks and teleosts.

Spatial and temporal closures may also be used to mitigate the risk to sharks in multi-species fisheries and may be the only way to protect some species that are particularly susceptible to certain gear types (e.g. hammerheads in the present study). Closures of inshore nursery areas have historically been used as a way of protecting sharks and have been considered a critical tool in managing shark populations (Olsen, 1959; McCandless *et al.*, 2007), although their usefulness has also been contested (Kinney and Simpfendorfer, 2009). Demonstrating the effectiveness of spatial closures for protecting wide-ranging, migratory species (e.g. the large coastal/semi pelagics and hammerheads) is challenging, although evidence suggests that these species may receive some benefits from spatial closures (Claudet *et al.*, 2010). Many of the patterns observed in this study (e.g. segregation by size, sex and habitat) may also present further opportunities for spatial or temporal closures. Capitalising on the seasonal nature of reproduction displayed by many elasmobranchs could be one way to achieve this. Most carcharhiniform sharks across northern Australia give birth during a relatively restricted time period over summer (Stevens and Wiley, 1986; Stevens and McLoughlin, 1991). This is also true within the GBRWHA, where neonates of a number of species such as *S. lewini*, *C. tilstoni*/*C. limbatus* and *C. fitzroyensis* were captured in intertidal zones at the beginning of summer, but apparently moved away from this zone soon afterwards. Temporal closures of nursery habitats during this brief period may therefore be effective in protecting both neonates and adult females of the medium coastal and large coastal/semi pelagic groups should they be vulnerable at this time.

Perhaps one of the most promising and as yet under-utilised risk mitigation strategies for sharks is sex-differential harvest. Strong segregation by size, sex and reproductive stage are well-documented characteristics of most shark populations (Springer, 1967; Sims, 2005). Mucientes *et al.* (2009), for example, reported strong sex segregation at large scales in the Pacific Ocean for shortfin mako, *Isurus oxyrinchus*, and suggested that differential exploitation of males was possible. Camhi *et al.* (1998) also suggested selective take of males only as a potential management measure for sharks. In the present study, sex-differential harvest was seen to be already occurring for some species. Where this was occurring for males (e.g. *R. acutus* and *S. lewini*) it may allow higher catches of these species with minimal effect on population growth rates. Conversely for species such as *S. mokarran*, the high bias towards catching females must also be recognised by managers as it is likely to have a disproportionately negative effect on the

population growth rate compared with equal harvest of both sexes. A sex differential harvest strategy would probably be most suited to the wide-ranging large coastal/semi pelagic species and hammerheads where sex segregation is likely to be occurring over large spatial scales. Such a management strategy could be formalised by restricting fishing to depths or regions where high numbers of males occur. Sex differential harvest is also appealing because, in fisheries where sharks are landed live (and assuming low post-release mortality), it can be incorporated without the need for any spatial closures, as sex can easily be established in sharks via examination of the pelvic fins. Enforcement of this management technique can also be achieved by requiring fishers to land sharks with pelvic fins intact (Walker, 2005a).

2.5 CONCLUSIONS

The present study was the most comprehensive observer survey ever applied to the Queensland ECIFF. The high elasmobranch species diversity, dominated by Carcharhiniformes, was characteristic of many inshore, tropical fisheries. The data-poor and highly complex nature of the ECIFF and similar fisheries means that quantitative, species-specific management is unlikely to be possible. However, close scrutiny of the catch characteristics show that there are many aspects of elasmobranch biology that are likely to be useful in designing management strategies that can mitigate the risk of overexploitation posed by such fisheries. These include the tendencies of elasmobranchs to show strong segregation by size and sex, along with the use of discrete areas during different life stages (e.g. nurseries) and the existence of many interspecific patterns in life history traits. Uptake and implementation of practical management strategies using this information is currently limited by a poor knowledge of life history and spatial ecology of sharks. Even across northern Australia where the tropical carcharhiniform shark assemblage and fisheries are arguably among the best-studied worldwide, age and growth information is currently available for only a limited number of species. The location and movement of adult stocks of many of the large, semi-pelagic species are also poorly documented. This highlights the ongoing requirement for the study of life history and spatial ecology in elasmobranchs.

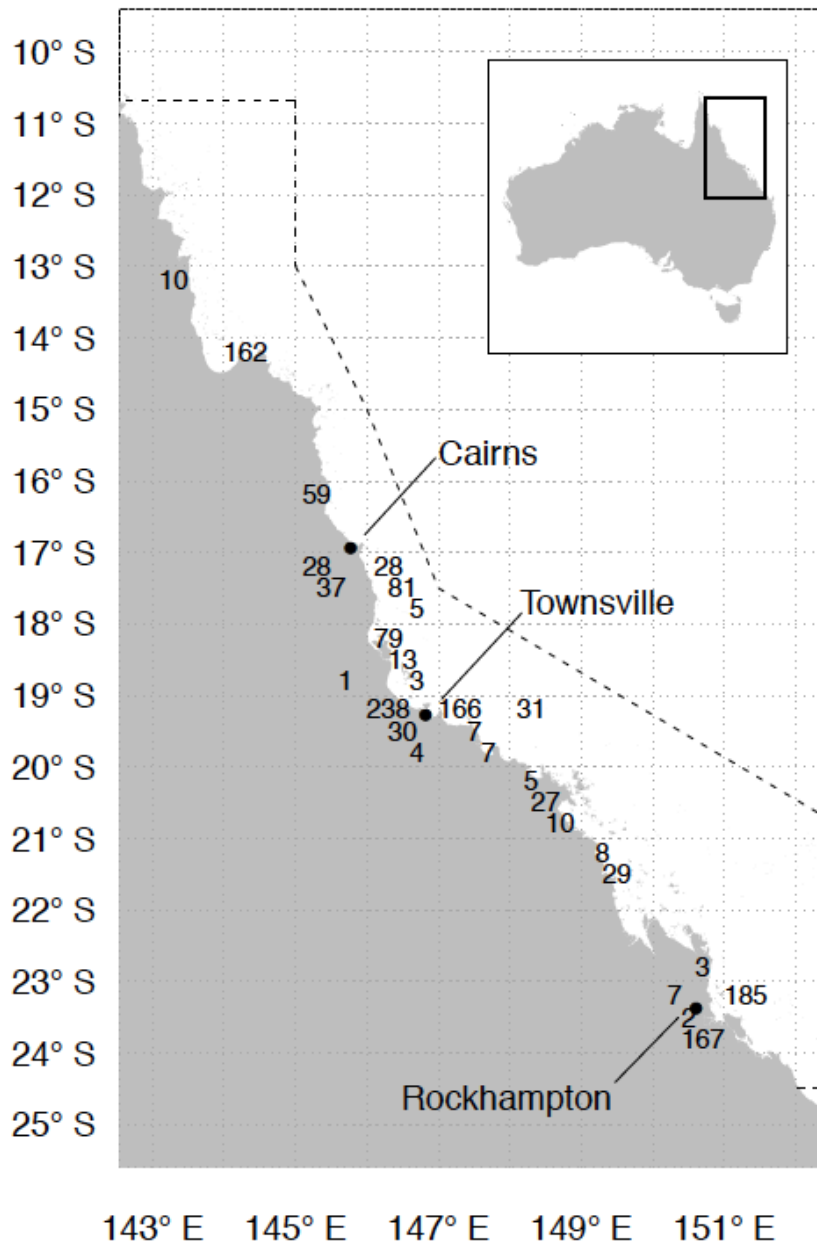


Figure 2.1. Study area showing observed fishing effort (km-net-hours) by one degree squares of latitude and longitude. Within each square observed effort is shown for the three zones: inshore (upper left), intertidal (centre), and river (bottom right). The dashed black line indicates the outer boundary of the GBRHWA.

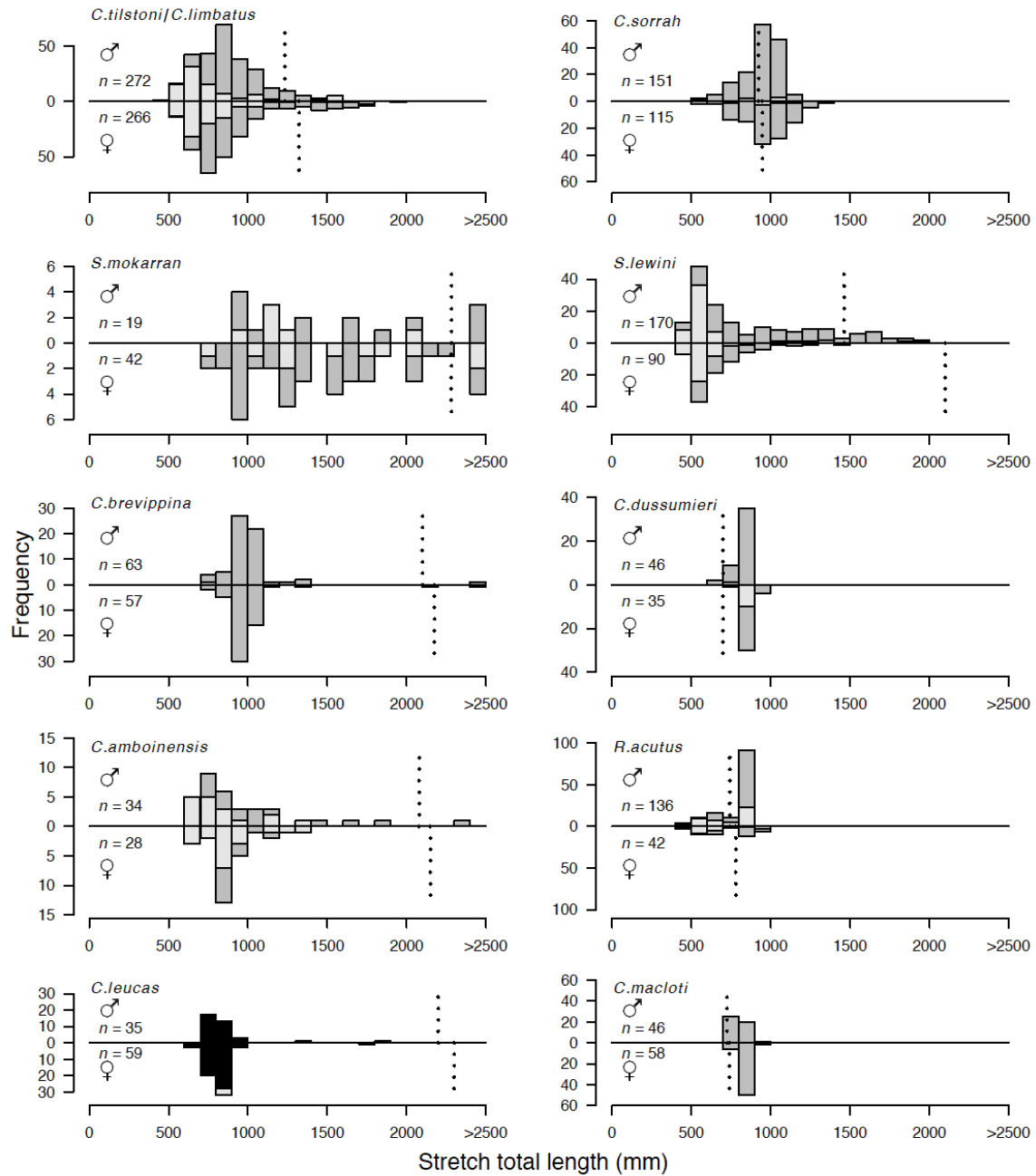


Figure 2.2. Length frequency distributions of the top 10 carcharhiniform sharks by weight (Table 2.4). Bar colour denotes the capture zone: solid black, river; dark grey, inshore; and light grey, intertidal. Length at 50% maturity is denoted by the dashed black line.

Table 2.1. Nominal fishery zones in the East Coast Inshore Finfish Fishery

	River	Intertidal	Inshore Coastal
Depth (m)	Any depth	0-2	2-25
Number of nets permitted	3	3	1
Total net length permitted (m)	150-360	600	600 (some to 1200)
Net mesh size (mm)	165-216	114-216	165
Principal target species	<i>Lates calcarifer</i>	<i>Eleutheronema tetradactylum</i> <i>Polydactylus macrochir</i> Mugilidae spp.	<i>Scomberomorus semifasciatus</i> Shark

Table 2.2. Total fishing effort observed from 2006–2009. The observer coverage was the most comprehensive fisheries observer program ever applied to the ECIFF, and included considerable coverage of fishing in river and intertidal zones, the most data-poor sectors of the fishery

	River				Intertidal				Inshore coastal					Grand total
	2007	2008	2009	Total	2007	2008	2009	Total	2006	2007	2008	2009	Total	
Trips	4	11	6	21	20	32	39	91	3	12	17	5	37	149
Duration (days)	4	32	14	50	26	45	45	116	11	49	51	20	131	297
Net shots	26	179	187	392	133	161	197	491	18	110	131	46	305	1188
Km net hours	11	70	121	202	103	73	61	237	120	397	306	190	1013	1452

Table 2.3. Catch composition of elasmobranchs caught by the East Coast Inshore Finfish Fishery in the Great Barrier Reef World Heritage Area. Data, grouped by order and sorted by numerical abundance, are from all 149 trips observed across the three nominal zones (river, intertidal, and inshore coastal). The dominance of carcharhiniform sharks in the elasmobranch component of the catch is typical of many tropical, inshore fisheries

Order	Family	Species	River	Intertidal	Inshore coastal	Component of catch (%)
Carcharhiniformes						94.5
	Carcharhinidae	<i>Carcharhinus altimus</i>			7	0.1
		<i>Carcharhinus amblyrhynchos</i>			7	0.1
		<i>Carcharhinus amblyrhynchoides</i>			23	0.3
		<i>Carcharhinus amboinensis</i>		38	53	1.3
		<i>Carcharhinus brevipinna</i>	1		227	3.3
		<i>Carcharhinus cautus</i>			3	<0.1
		<i>Carcharhinus dussumieri</i>		11	247	3.8
		<i>Carcharhinus fitzroyensis</i>		41	164	3.0
		<i>Carcharhinus leucas</i>	83	10	3	1.4
		<i>Carcharhinus macloti</i>			275	4.0
		<i>Carcharhinus melanopterus</i>	1	46	27	1.1
		<i>Carcharhinus sorrah</i>		12	995	14.7
		<i>Carcharhinus</i> spp.			843	12.3
		<i>Carcharhinus tilstoni</i> / <i>C. limbatus</i>		164	1154	19.3
		<i>Galeocerdo cuvier</i>		1	19	0.3
		<i>Loxodon macrorhinus</i>		1	331	4.9
		<i>Negaprion acutidens</i>	11	7	3	0.3
		<i>Rhizoprionodon acutus</i>	1	82	457	7.9
		<i>Rhizoprionodon taylori</i>		45	260	4.5
		<i>Triaenodon obesus</i>			2	<0.1
	Hemigaleidae	<i>Hemipristis elongata</i>		4	17	0.3
		<i>Hemigaleus australiensis</i>		3	7	0.1
	Sphyrnidae	<i>Eusphyrna blochii</i>		6	18	0.4
		<i>Sphyrna lewini</i>	1	128	475	8.8
		<i>Sphyrna mokarran</i>	1	15	86	1.5
		<i>Sphyrna</i> spp.			34	0.5
Rajiformes						3.9
	Dasyatidae	<i>Dasyatis fluviatorum</i>		4		0.1
		<i>Himantura astra</i>		1		<0.1
		Unidentified ray	9	17	7	0.5
	Mobulidae	<i>Manta</i> spp.			3	<0.1
		<i>Mobula</i> spp.			3	<0.1
	Myliobatidae	<i>Aetobatus narinari</i>		8	13	0.3
		<i>Aetomylaeus nichofii</i>			2	<0.1
		<i>Aetomylaeus vespertilio</i>			1	<0.1
		<i>Rhinoptera</i> spp.		93	6	1.4
		Unidentified eagle ray			3	<0.1
	Rhinobatidae	<i>Glaucostegus typus</i>	4	20	3	0.4
	Rhynchobatidae	<i>Rhynchobatus</i> spp.	1	14	53	1.0
Pristiformes						1.2
	Pristidae	<i>Anoxypristis cuspidata</i>		40	35	1.1
		<i>Pristis zijsron</i>	1	4	2	0.1
Orectolobiformes						0.3

	Stegastomatidae	<i>Stegostoma fasciatum</i>		11	0.2
	Hemiscylliidae	<i>Chiloscyllium punctatum</i>	3	5	0.1
	Brachaeluridae	<i>Brachaelurus colcloughi</i>		1	<0.1
Unknown				11	0.2
Total			114	829	5885

Table 2.4. Catch per unit effort and catch composition of carcharhiniform sharks. Species are sorted by the proportion of the total observed catch across all habitats by weight. Data are from a subsample of 126 observer trips where all individuals were identified to species level. Blank records indicate no recorded occurrence in catch

Species	Catch				Catch per unit effort					
	Mean size (mm)	Mean weight (kg)	Number (%)	Weight (%)	River (individuals.km-net-hour ⁻¹)	Intertidal	Inshore coastal	River	Intertidal	Inshore coastal
<i>Carcharhinus tilstoni/C. limbatus</i>	910	4.1	28.2	30.6		0.8	1.3		3.3	5.4
<i>Carcharhinus sorrah</i>	963	4.7	16.6	20.5		0.1	0.9		0.3	4.3
<i>Sphyrna mokarran</i>	1563	15.5	2.4	9.7	<0.1	0.1	0.1	0.1	1.2	1.6
<i>Sphyrna lewini</i>	809	2.3	11.4	6.8		0.5	0.5		1.0	1.1
<i>Carcharhinus brevipinna</i>	943	3.7	6.7	6.5			0.4			1.4
<i>Carcharhinus amboinensis</i>	955	5.9	2.4	3.9		0.2	0.1		1.1	0.4
<i>Rhizoprionodon acutus</i>	746	1.8	7.8	3.8		0.3	0.3		0.6	0.6
<i>Carcharhinus leucas</i>	879	4.2	2.7	3.7	0.4	<0.1		1.7	0.1	
<i>Carcharhinus dussumieri</i>	829	3.0	4.8	2.9		0.1	0.3		0.2	0.8
<i>Carcharhinus macloti</i>	836	2.6	3.7	2.5			0.2			0.5
<i>Rhizoprionodon taylori</i>	623	1.1	6.9	1.9		0.2	0.3		0.2	0.3
<i>Carcharhinus melanopterus</i>	753	2.5	2.4	1.6	<0.1	0.2	<0.1	<0.1	0.6	0.1
<i>Carcharhinus fitzroyensis</i>	881	4.0	1.4	1.5		0.2			0.8	
<i>Hemipristis elongata</i>	1318	9.7	0.5	1.2		<0.1	<0.1		0.2	0.2
<i>Galeocerdo cuvier</i>	1283	8.8	0.4	1.0		<0.1	<0.1		<0.1	0.2
<i>Eusphyra blochii</i>	1363	8.3	0.4	0.9		<0.1	<0.1		0.3	0.1
<i>Negaprion acutidens</i>	891	3.1	0.7	0.6	0.1	<0.1	<0.1	0.2	0.1	
<i>Hemigaleus australiensis</i>	940	3.1	0.3	0.3		<0.1	<0.1		<0.1	<0.1
<i>Carcharhinus caudatus</i>	955	5.7	0.1	0.2			<0.1			<0.1
<i>Carcharhinus altimus</i>	839	2.3	0.2	0.1			<0.1			<0.1
<i>Loxodon macrorhinus</i>	872	2.3	<0.1	<0.1		<0.1			<0.1	
Total					0.5	2.8	4.5	2.0	10.1	17.1

Table 2.5. Tabulation of sex-specific length at capture details, sex ratio and the percentage of catch mature or neonate. The results of Kolmogorov-Smirnov tests comparing length frequency distributions of males and females and chi-squared tests on the sex ratio of the catch are also given. Where only a single length measurement was available it was given as maximum size at capture and other fields were left blank

Species	Length (mm)						KS-Test P	Sex ratio (F/M)	Chi-sq. test P	Mature animals (%)			Neonates (%)
	Male			Female						Male	Female	Combined	
	Min.	Max.	Mean	Min.	Max.	Mean							
<i>Carcharhinus tilstoni/C. limbatus</i>	580	1600	877	570	1930	904	0.26	0.98	0.80	3.3	5.8	9.1	5.2
<i>Carcharhinus sorrah</i>	580	1130	939	630	1301	966	0.01	0.76	0.03	36.1	24.8	60.9	0.0
<i>Sphyrna mokarran</i>	916	2830	1542	795	4280	1544	0.95	2.21	<0.01	4.9	6.6	11.5	0.0
<i>Sphyrna lewini</i>	465	1930	893	465	1236	662	<0.01	0.53	<0.01	8.5	0.0	8.5	8.9
<i>Carcharhinus brevipinna</i>	771	2480	1016	763	2830	1019	0.38	0.90	0.58	0.8	0.8	1.7	0.0
<i>Carcharhinus dussumieri</i>	670	892	824	791	915	853	<0.01	0.74	0.19	54.9	42.7	97.6	0.0
<i>Carcharhinus amboinensis</i>	663	2400	994	649	1380	915	0.34	0.82	0.45	1.6	0.0	1.6	17.6
<i>Rhizoprionodon acutus</i>	385	931	779	440	940	713	<0.01	0.31	<0.01	56.2	11.2	67.4	0.6
<i>Carcharhinus leucas</i>	715	1850	852	660	1750	830	0.47	1.69	0.01	0.0	0.0	0.0	62.1
<i>Carcharhinus macroti</i>	706	980	794	742	910	850	<0.01	1.26	0.24	43.3	55.8	99.0	0.0
<i>Rhizoprionodon taylori</i>	456	730	637	400	796	686	<0.01	1.98	<0.01	22.8	60.8	83.5	0.0
<i>Carcharhinus melanopterus</i>	543	1390	750	514	1600	723	0.67	1.58	0.08	4.8	3.2	8.1	4.8
<i>Carcharhinus fitzroyensis</i>	505	1070	765	520	1304	849	0.36	1.20	0.46	15.2	19.7	34.8	5.5
<i>Hemipristis elongatus</i>	788	1690	1288	1310	2003	1431	0.13	0.45	0.13	43.8	25.0	68.8	0.0
<i>Galeocerdo cuvier</i>	1060	1123	1088	965	1090	1019		1.00		0.0	0.0	0.0	
<i>Eusphyra blochii</i>	633	1720	1106	1428	1700	1520		0.57		40.0	30.0	70.0	0.0
<i>Negaprion acutidens</i>	755	1000	867	650	1790	901		1.43		0.0	0.0	0.0	15.0
<i>Hemigaleus australiensis</i>	870	1060	966		1060			0.10		90.9	9.1	100.0	0.0
<i>Carcharhinus cautus</i>		1025			885			1.00		50.0	0.0	50.0	0.0
<i>Carcharhinus altimus</i>	795	928	849	735	925	834		2.00		0.0	0.0	0.0	0.0
<i>Loxodon macrorhinus</i>		990						0.00		100.0	0.0	100.0	0.0

Table 2.6. Groupings of similarly susceptible shark species caught in the East Coast Inshore Finfish Fishery

Life stages susceptible	Small coastal (<1000 mm) Adult only	Medium coastal (1000-2000 mm) All sizes	Large coastal, semi-pelagic (>2000 mm) Neonate and juvenile	Hammerheads All sizes
	<i>Carcharhinus dussumieri</i>	<i>Carcharhinus cautus</i>	<i>Carcharhinus altimus</i>	<i>Eusyphra blochii</i>
	<i>Carcharhinus macroti</i>	<i>Carcharhinus fitzroyensis</i>	<i>Carcharhinus amboinensis</i>	<i>Sphyrna lewini</i>
	<i>Hemigaleus australiensis</i>	<i>Carcharhinus melanopterus</i>	<i>Carcharhinus brevipinna</i>	<i>Sphyrna mokarran</i>
	<i>Loxodon macrorhinus</i>	<i>Carcharhinus sorrah</i>	<i>Carcharhinus leucas</i>	
	<i>Rhizoprionodon acutus</i>	<i>Carcharhinus tilstoni</i>	<i>Carcharhinus limbatus</i>	
	<i>Rhizoprionodon taylori</i>	<i>Hemipristis elongata</i>	<i>Galeocerdo cuvier</i>	
			<i>Negaprion acutidens</i>	

Chapter 3. Improving age, growth, and maturity estimates for aseasonally reproducing chondrichthyans



Plate 3. A tagged and calcein marked milk shark, *Rhizoprionodon acutus*, released into Cleveland Bay (July 2008).

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3.1 INTRODUCTION

Reproductive cycles in chondrichthyan fishes can be placed into three broad categories: species with a well-defined annual or biennial cycle (seasonal), species with a partially-defined annual cycle with one or more seasonal peaks (partially seasonal), and species that reproduce throughout the year (aseasonal) (Wourms, 1977). While a seasonal cycle is dominant among chondrichthyan species studied to date, aseasonal reproducers are not uncommon and can be found in most orders of sharks, rays, and chimaeras (Yano and Tanaka, 1988; Tanaka *et al.*, 1990; Chen *et al.*, 1997; Watson and Smale, 1998; Sulikowski *et al.*, 2007; Awruch *et al.*, 2008; Last and Stevens, 2009). Reproductive cycles can be highly variable, even intraspecifically at relatively small geographic scales (Yamaguchi *et al.*, 2000). While there seem to be no fixed rules which govern where a given reproductive cycle will occur, aseasonal cycles seem to occur more frequently in deepwater and tropical species.

The study of growth in fishes is a fundamental component of fisheries science, and maximising accuracy in age determination is critical for obtaining the best results from stock assessments (Quinn and Deriso, 1999; Cailliet *et al.*, 2006). Age in chondrichthyan species is usually determined by counting pairs of opaque and translucent bands deposited on calcified structures such as the vertebrae, dorsal spines, or caudal thorns (Cailliet and Goldman, 2004). The timing and periodicity of translucent band deposition must be validated for each species, but timing is typically during winter or after reproduction, and periodicity is typically annual or biannual e.g. (McAuley *et al.*, 2006; Anislado-Tolentino *et al.*, 2008). Most chondrichthyan species aged to date are seasonal reproducers and therefore have a relatively well defined birth date (Cailliet and Goldman, 2004). As such, the age of the animal at the first band pair or increment can be determined with reasonable accuracy. In aseasonally reproducing species however, birth can occur throughout the year, so the age at first band (AAFB) is unknown. Consequently, if a fixed AAFB is used there will be up to 12 months error for an individual animal, and potentially some level of bias depending on what value AAFB is fixed at.

For example, in growth studies of *Carcharhinus falciformis* in the Pacific Ocean, Oshitani *et al* (2003) and Joung *et al* (2008) gave all animals in the population a fixed birth date of June 1. Annual, translucent band formation was verified to occur during May and January respectively for each study. Logically, the AAFB for Oshitani would then be 11 months, and 7 months for

Joung. However, if the reproductive biology of *C. falciformis* were actually aseasonal, as has been reported by some studies in the Pacific (Strasburg, 1958; Stevens, 1984; White *et al.*, 2006), then probability of birth at any time of the year would be equal, and the mean AAFB would actually be 6 months. As such, a bias of +5 months and +1 month would be introduced by fixing the birth date. In any case, both authors apparently assumed the first band represented 1 year of growth, ignoring its timing in relation to the birth date that they had assigned.

The former examples are typical of most growth studies on aseasonal species, which have not considered the potential impact of this mode of reproduction (Liu *et al.*, 1999; Watson and Smale, 1999). Indeed, this approach may be justifiable to some extent as most chondrichthyans are relatively slow growing. As such, the error caused by assigning a fixed birth date may quickly become negligible in the context of the stochastic processes and measurement errors that are often unavoidably associated with growth studies. However, for smaller, fast-growing species the implications of fixing the AAFB at an incorrect value may be much more profound.

The seven species of the genus *Rhizoprionodon* (Carcharhiniformes: Carcharhinidae) are a useful case in point. All are slender-bodied sharks occurring in tropical and sub-tropical inshore and continental shelf habitat to 200 m (Compagno *et al.*, 2005). *Rhizoprionodon* species have some of the highest growth rates calculated for elasmobranchs, growing by as much as 140% of their size at birth in the first year of life (Simpfendorfer, 1993; Carlson and Baremore, 2003; Loefer and Sedberry, 2003). For species such as these, where growth to asymptotic size occurs very rapidly, maximising the accuracy of early age estimates is particularly important.

The milk shark, *Rhizoprionodon acutus*, is the most widely distributed of all *Rhizoprionodon* species and has a continuous distribution from Indo-West Pacific region throughout the Indian Ocean. Isolated populations are also found in the east Atlantic and Mediterranean (Compagno *et al.*, 2005). Throughout its range it is of high importance to commercial and artisanal fisheries where it is often the most abundant species caught (Krishnamoorthi and Jagadis, 1986; Kasim, 1991; Stevens and McLoughlin, 1991; Henderson *et al.*, 2007). The life history of this species varies greatly with geographic location – size at maturity occurs at 650-950 mm and size at birth is 300-500mm. The reproductive cycle ranges from seasonal (Bass *et al.*, 1975; Capapé *et al.*, 2006), to partially seasonal (Krishnamoorthi and Jagadis, 1986; Henderson *et al.*, 2006), to fully aseasonal within northern Australian waters (Stevens and McLoughlin, 1991), the location of the

present study. Despite its commercial importance, age and growth of this species has not been attempted using vertebral ageing methods.

The aims of the present study were therefore to (1) investigate the effect of an aseasonal reproductive cycle on age and growth parameters and develop a protocol to minimise errors associated with this reproductive mode, and (2) determine age, growth and maturity parameters of *R. acutus* in north-eastern Australian waters.

3.2 METHODS

3.2.1 Sample collection

Samples were collected from March 2007 to November 2010 and were mostly sourced from commercial net fishers targeting shark (primarily *Carcharhinus tilstoni* and *Carcharhinus sorrah*), grey mackerel (*Scomberomorus semifasciatus*), barramundi (*Lates calcarifer*) and threadfin salmon (polynemids *Eleutheronema tetradactylum* and *Polydactylus macrochir*) in inshore waters along the north-eastern coast of Australia (from 10.5°S to 26°S) (Figure 3.1). In reflection of the diversity of body forms represented by the targeted species, fishers utilise a range of different mesh sizes ranging from a minimum of 114 mm (4.5 inch), to a maximum of 165 mm (6.5 inch) stretched mesh. *Rhizoprionodon acutus* were caught and sampled from a range of habitats including shallow inter-tidal foreshores (<1 m depth), coastal embayment waters (1 to 10 m depth) and coastal offshore waters (11 to 25 m). Fishers commonly process captured shark at sea by removing the head, belly flap and viscera, so the collection of biological data also usually occurred at sea. In addition to the samples collected from commercial fishers, samples were collected opportunistically via experimental multihook longline, gillnet, trawl, and rod and reel sampling.

The stretch-total length (STL) of sharks was measured in mm following Compagno (1984) by placing the animal belly down and depressing the upper lobe of the caudal fin into line with the body axis. Additional measurements of fork length (FL), and pre-caudal (PCL) length were recorded for a subsample of animals. The relationships between STL, FL and PCL for sexes combined were:

$$STL = 30.91 + 1.19 \cdot FL \quad (r^2 = 0.99, p < 0.001, d.f. = 252)$$

$$STL = 48.79 + 1.27 \cdot PCL \quad (r^2 = 0.99, p < 0.001, d.f. = 153)$$

3.2.2 Vertebral processing and analysis

A section of five vertebrae was removed from the anterior region of the vertebral column between the gills and the first dorsal fin and stored frozen. Latter processing used a scalpel to remove the neural and haemal arches and scrape off tissue leaving only the vertebral centra. Centra were then soaked in a solution of 5% sodium hypochlorite (bleach) for approximately 30 minutes to remove remaining tissue, rinsed thoroughly under tap water, and placed in a drying oven at 60°C for 24 hours. One of the five centra prepared from each individual was randomly selected for ageing. A 400–600µm longitudinal section was taken through the focus of the centrum using a slow-speed saw with a diamond-tipped blade (Beuhler, Illinois, USA) (Cailliet and Goldman, 2004). The resulting sections were fixed to glass slides using Crystalbond adhesive (SPI Supplies, Pennsylvania, USA).

Sectioned vertebrae centra were examined under a dissecting microscope using transmitted light and photographed using a digital camera. The age of an animal was determined by counting the pairs of opaque and translucent (hyper- and hypomineralised) bands deposited on the corpus calcareum (Figure 3.2). The birth mark was identifiable by a change of angle on the corpus calcareum. Any banding that occurred before the birth mark, i.e. pre-birth marks (Goldman and Musick, 2006) was not counted. Prior to ageing all centra, a random sub-sample were read by two readers (AH and CS) to ensure that a consensus was reached regarding interpretation of the banding pattern. A single reader (AH) then read each centrum twice. Precision between reads was evaluated using Chang's (1982) method of the coefficient of variation (CV) and percent agreement following the method of Goldman and Musick (2006). Bias between reads was evaluated statistically using Bowker's test of symmetry (Evans and Hoenig, 1998). Age-bias plots were used to visualise precision and bias and were overplotted with age-specific agreements from the contingency tables (Francis *et al.*, 2007).

Because of small sample sizes, back-calculation, a method for describing the growth history of each individual sampled (Cailliet and Goldman, 2004), was used to estimate lengths-at-previous-ages of all individuals in this study. Back-calculation measurements were taken from photos of centra using Image Pro Plus image analysis software (Media Cybernetics, Maryland, USA) by taking a transect from the focus of the vertebrae through the widest part of the corpus calcareum

(Figure 2). The centrum radius (CR), distance to birth mark, and distance to each growth band pair were measured. Numerous back-calculation methods exist and the appropriate method depends on the relationship between length and vertebrae centrum radius. Following Goldman and Musick (2006), four back-calculation models were trialled: Dahl-Lee direct proportions method, linear modified Dahl-Lee method, quadratic modified Dahl-Lee method, and the biological-intercept Fraser Lee method. The most appropriate method was chosen by comparing the back-calculated length-at-age data generated by each model with observed length-at-age data.

A multi-model, information theoretic approach (AIC MMI) was taken to modelling growth (Burnham and Anderson, 2001). This method has recently been proposed as an improvement on *a priori* use of the von Bertalanffy growth function (Katsanevakis and Maravelias, 2008; Thorson and Simpfendorfer, 2009). A set of five candidate models $g_i(i=1-5)$ was chosen based on Thorson and Simpfendorfer (2009) (Table 3.1). These included a 3 parameter version of the von Bertalanffy model (VB3), a 2 parameter version of the von Bertalanffy model with a fixed size at birth (VB2), the Gompertz model, a logistic model, and the Schnute model. Each of the candidate models represents an alternative hypothesis for growth, and all have been used in chondrichthyan studies. Because all models assume normally distributed errors and constant variance, the method of least squares was used to fit models. Best-fit parameter estimates were obtained using the Nelder Mead algorithm in “Optim”, a general purpose optimisation function in the statistical package “R” (R Development Core Team, 2009). Standard errors for the regression parameters were computed by passing the best-fit parameter estimates to the “nls” function in R. Upper and lower confidence intervals on asymptotic length (parameter β_1) were estimated as $\beta_1 \pm t_{d.f., 0.025} S.E.(\beta_1)$.

Model performance was evaluated using Akaike’s Information Criteria (AIC). The small sample, bias adjustment form of AIC was calculated as

$$AIC_c = AIC + \frac{2K(K+1)}{n-K-1},$$

where K is the total number of estimated parameters + 1 for variance (σ^2), n is the samples size, and $AIC = n \log(\sigma^2) + 2K$. Variance was calculated as $\sigma^2 = \frac{RSS}{n}$ where RSS is the sum of the squared residuals. The best model was the one with the lowest AIC_c value, AIC_{\min} . AIC differences were calculated as $\Delta_i = AIC_{c,i} - AIC_{\min}$, and used to rank the support of the

remaining models relative to the best model. Models with Δ_i of 0-2 had substantial support, while models with Δ_i of 4-7 had considerably less support. Models with $\Delta_i > 10$ had essentially no support (Burnham and Anderson, 2002). Akaike weights (w_i), the weight of evidence in favour of a model being the best model in the set of candidate models, were calculated as

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{i=1}^5 \exp(-\frac{1}{2}\Delta_i)}.$$

Model averaging was carried out on parameter β_1 , asymptotic length, as this parameter is common to all models. Model average asymptotic length was calculated as

$$\bar{\beta}_1 = \sum_{i=1}^5 w_i \beta_{1,i}$$

The unconditional standard error of $\bar{\beta}_1$ was estimated as

$$S.E.(\bar{\beta}_1) = \sum_{i=1}^5 w_i \sqrt{\text{var}(\beta_{1,i}|g_i) + (\beta_{1,i} - \bar{\beta}_1)^2},$$

where $\text{var}(\beta_{1,i}|g_i)$ is the variance of asymptotic length for model g_i , conditional on the model.

Model averaged length-at-age was calculated by taking the weighted average of predicted length $L(t)$ from all models, using w_i as the weights. As there was only a single parameter (asymptotic size) that was common to all models, the slope of each model at birth and maturity was calculated as an additional measure of growth rate (Thorson and Simpfendorfer, 2009). Model averaged growth rate at birth (dL/dt_0) and growth rate at maturity (dL/dt_{MAT}) were calculated as per model average asymptotic length. Age at maturity data used was calculated as described below.

3.2.3 Verification of growth band periodicity

Relative marginal increment (RMI) analysis was used to verify the timing and frequency of translucent growth band deposition (Cailliet and Goldman, 2004). RMI was calculated as

$RMI = (CR - R_n)/(R_n - R_{n-1})$, where CR is the vertebral radius measured from the focus to the edge of the corpus calcareum, R_n is the radius of the ultimate band pair, and R_{n-1} is the radius to the next band pair or birth mark (Natanson *et al.*, 1995). Age 0 animals were excluded because they lacked any fully formed band pairs. Because of a lack of samples, both sexes and all age classes were pooled.

3.2.4 Investigating the effects of aseasonal reproduction on modelling growth

To investigate the effects of aseasonal reproduction, growth was analysed using three different values for the AAFB in the back-calculated length-at-age dataset: (1) unadjusted values, (2) mean-adjusted values and (3) individual-adjusted values. In the unadjusted analysis, all band-pairs were assumed to represent 1 year of growth. As such, the AAFB was left unadjusted at 1 year, and the original band-pair count was the age of the fish. This is an approach typical of many chondrichthyan growth studies, irrespective of reproductive seasonality. In the mean-adjusted analysis, the AAFB was adjusted to the mean-value for the population. In an aseasonal population, the probability of birth at any given time during the year is equal and there is no mean birth date. As such, the AAFB will also have an equal probability of taking any value from 0-12 months. Therefore the mean AAFB will be 6 months, so the AAFB for all animals was adjusted to 0.5 years.

Assigning the appropriate mean AAFB removes bias from the growth analysis caused by aseasonal reproduction. However, it does not reduce the level of error associated with having a first band that can be formed at any stage during the first year of life. The third, individual-adjusted analysis was therefore designed to minimise error in estimates of first year growth. The first growth increment (FGI), distance from the birth mark (B) to the first band (1) (Figure 3.2), was measured for all individuals with at least one completed band pair. The 97.5th percentile of the FGI distribution was assumed to represent the maximum extent of growth possible before the first band is formed (i.e. animals born in July and not forming a first band until the following July). The AAFB for individual animals was then calculated as

$$AAFB = \frac{FGI}{FGI_{MAX}}$$

where FGI_{MAX} is the maximum extent of growth possible in the first year.

The performance of each of the above methods was evaluated by comparing asymptotic size, growth rate at birth, and growth rate at maturity. A final choice on the most appropriate method was based on biological realism and the level of uncertainty around asymptotic size.

3.2.5 Maturity analysis

Reproductive staging of animals was determined based on the descriptions of Walker (2005). Maturity in males was determined by examining the claspers: stage 1 (immature), claspers pliable with no calcification; stage 2 (immature), claspers partly calcified; stage 3 (mature), claspers fully calcified. Female maturity was determined by visual examination of the uterus: stage 1 (immature), uniformly thin tubular structure; stage 2 (immature), thin tubular structure partly enlarged posteriorly; stage 3 (mature) uniformly enlarged tubular structure; stage 4 (mature), in utero eggs present without macroscopically visible embryos present; stage 5 (mature), in utero embryos macroscopically visible; stage 6 (mature), enlarged tubular structure distended.

Maturity stage data was converted into binary form (immature = 0, mature = 1) and grouped in 20 mm length bins for determination of length at maturity. The expected proportion of mature sharks in each size class, $P(L)$, was estimated using a logistic regression model (Roa *et al.*, 1999):

$$(1) \quad P(L) = \frac{\alpha}{1 + e^{\beta_0 + \beta_1 L}}$$

where α is the asymptote (fixed at 1), β_0 is the intercept, and β_1 is the slope. This model was chosen because of its widespread use in estimating size at maturity, especially in chondrichthyan fishes (e.g. Braccini and Chiamonte, 2002; Walker, 2005b; Ebert *et al.*, 2007; McAuley *et al.*, 2007b). Parameters β_0 and β_1 were estimated using Optim by minimising the negative log-likelihood function for binomially distributed data (Welch and Foucher, 1988):

$$(2) \quad -l(\beta_0, \beta_1) = -\sum [(n_{m,L}) \ln(P(L)) + (n_L - n_{m,L}) \ln(1 - P(L))]$$

where the total number of animals in size class L is n_L , the number of mature animals in size class L is $n_{m,L}$, and $P(L)$ is given by (1). The length at which 50% of the population were mature ($L_{0.5}$) was calculated as $-\beta_0 \times \beta_1^{-1}$ (McAuley *et al.*, 2007b). To describe the uncertainty surrounding the $L_{0.5}$ estimate, size at maturity data were randomly re-sampled with replacement 10,000 times. For each resampled dataset, the $L_{0.5}$ statistic was recalculated. The bias-corrected-accelerated (BCA) method of Efron and Tibshirani (1993) for non-parametric bootstrapped data was used to place 95% confidence intervals around the $L_{0.5}$ estimate. Age at maturity was determined by substituting age in years (A) in place of length (L) in the above equations. Age at

maturity estimates were calculated for each of the three growth analyses. Maturity stage data were grouped in 0.2 year bins for the individual-adjusted AAFB dataset.

3.3 RESULTS

3.3.1 *Centrum morphology*

The relationship between CR and STL was non-linear and best described by a quadratic model $STL = -31.09 \cdot CR^2 + 382.27 \cdot CR - 291.12$ ($r^2 = 0.91$, $p < 0.001$, $d.f. = 227$). Despite this, mean back-calculated lengths-at-age using the Dahl Lee linear-modified back-calculation method were closest to observed mean lengths-at-age. The linear relationship between STL and CR was $STL = 131.04 \cdot CR + 181.29$ ($r^2 = 0.88$, $p < 0.001$, $d.f. = 228$). The banding pattern on centra was typified by a wide opaque band followed by a very narrow translucent band (Figure 3.2). Mean back-calculated size at birth \pm SD was 421 ± 32 mm. This is slightly larger than two neonates sampled with unhealed umbilical scars which were 385 mm, and also larger than the size at birth of *R. acutus* in northern Australia which is 340-380 mm (Stevens and McLoughlin, 1991). This indicates that the birth mark is probably not formed (or not visible) until several weeks or months after birth, as has been suggested for other species of this genus (Simpfendorfer, 1993; Loefer and Sedberry, 2003). A mean back-calculated size at birth (or rather size at birth-mark formation) of 421 mm was used as the fixed size at birth in the VB2 model.

3.3.2 *Precision and bias in age estimation*

The percent agreement to within 1 growth band pair between Read 1 and Read 2 was 92%. However, Chang's coefficient of variation was 22.08% indicating that there was still considerable error between the two reads. Bowker's test of symmetry confirmed that there was also systematic bias present between the two reads ($\chi^2 = 44.36$, $d.f. = 11$, $p < 0.001$). This can be seen clearly in the age-bias plot (Figure 3.3) and is almost entirely centred on individuals with growth band pair counts of 3 and 4 which were aged 2 and 3 in Read 1. Given that the magnitude of bias was low, and the CV was within the usual range for elasmobranch studies, Read 2 was considered by both authors as an acceptable interpretation of the centra and used as the final age.

3.3.3 Verification of growth band periodicity

Relative marginal increment (RMI) data were available from 167 individuals from 10 months of the year (Figure 3.4), however only 4 months had sample sizes >10. *Rhizoprionodon acutus* forms narrow translucent bands throughout the year and there is considerable variation in the timing of band formation and individual RMI values. Mean RMI increased from March, reached a peak in July, and decreased until November. A Kruskal-Wallis one-way test by ranks revealed that RMI varied significantly between months ($\chi^2=16.415$, d.f.=8, $p=0.037$). The trend in mean RMI is therefore supportive of an annual peak in translucent band formation during winter. A date of July 1st was therefore taken as the mean date of translucent band formation.

3.4 Examining the effect of an aseasonal reproductive cycle on growth and maturity

Vertebra centra were processed from 71 females ranging from 443-940 mm and 160 males ranging from 385-890 mm. Back-calculation yielded 196 length-at-age data points for females and 507 length-at-age data points for males (Figure 3.5). Length and maturity stage data were available for 62 females (443–940 mm) and 176 males (385–931 mm). Length at 50% maturity for females and males was 780 and 742 mm, respectively (Figure 3.6 a and b). Age and maturity stage data were available for 59 females (443–940mm) and 153 males (385–890mm).

Using an unadjusted AAFB (Figure 3.5 a and b), the logistic model had the most support given data for both females and males ($w=50\%$ and 57.8% , Table 3.3). The Gompertz model also had considerable support ($w=24.3\%$ and 22.6%). Asymptotic sizes for females and males in the unadjusted dataset were 881 mm and 848 mm. Growth rates at maturity were ~60% of growth rate at birth (Table 2), indicating that considerable growth occurred after maturity was reached. A clear asymptote was not reached in males, and females reached asymptotic size in only the very oldest age classes. Age at 50% maturity was reached at 2.1 years for females and 1.5 years for males (Figure 3.6 c and d). The oldest females and males aged were 8 and 5 years.

Using a mean-adjusted AAFB (Figure 3.5 b and c), the VB2 and VB3 curves had by far the greatest support given the data (Table 3.2). All other models had essentially no support. Both VB functions had similar best-fit parameters (Table 3.3), although the VB2 had the greatest weighting in the MMI framework as it had fewer parameters. Asymptotic sizes reached were 844 mm for females and 807 mm for males, considerably smaller than the largest animals aged. Growth rates for both sexes were extremely fast initially, however upon reaching maturity had

slowed to ~30% of the growth rate at birth. Both sexes rapidly grew to an asymptotic size, after which very little growth occurred. Age at maturity estimates using the mean-adjusted AAFB were 1.6 years for females and 1 year for males (Figure 3.6 c and d). Maximum longevity estimates were 7.5 years for females and 4.5 years for males.

Distributions of the first growth increment were estimated from 34 females and 104 males that had at least one growth band pair (Figure 3.7). Male $FGI \pm SE$ was normally distributed with a mean of 1.21 ± 0.05 mm, corresponding to an absolute mean growth of approximately 210mm. For females, a normal distribution for FGI was not apparent, perhaps due to the small sample size. Given that male FGI was normally distributed, and in the absence of more data, we assumed that female FGI was similarly normally distributed. Mean $FGI \pm SE$ for females was 1.01 ± 0.06 mm, corresponding to an absolute mean growth of approximately 180mm. The 97.5th percentiles of a normal distribution fitted to females and males were 1.65 mm and 2.17 mm. These values correspond to an upper limit of first year growth of approximately 400 mm for females and 460 mm for males.

Results using an individual-adjusted AAFB were similar to, but slightly more conservative than the mean-adjusted AAFB (Figure 3.7 e and f). In both sexes, the VB functions again had by far the greatest support in the MMI framework (Table 3.3). The VB2 function again outperformed the VB3 function as it had fewer parameters. Female and male asymptotic sizes reached were 859 mm and 821 mm. Both sexes grew rapidly at birth, quickly reaching asymptotic size. Age at 50% maturity was 1.8 years for females and 1.1 years for males (Figure 3.6 c and d). The ages of the oldest animals using this method were 8.1 years for females and 4.5 years for males.

A comparison of the three methods for analysing growth can be seen in Figure 3.8. The mean- and individual-adjusted AAFB datasets produced similar shaped curves that fit well to the von Bertalanffy models. The unadjusted AAFB dataset suggested slower, consistent, growth throughout life and fit best to logistic and Gompertz growth models. Standard errors around the model averaged asymptotic size were largest in the unadjusted AAFB analysis (Table 3.2). For males, the individual-adjusted analysis had the smallest standard error, while for females the mean-adjusted analysis had the smallest standard error. In each analysis, females grew slower than males, but attained a larger asymptotic size.

3.4 DISCUSSION

While several studies have aged aseasonally reproducing elasmobranchs, this is the first study to explicitly account for this mode of reproduction. The results demonstrate how adjustment of ages can result in substantial changes to life history parameters for fast-growing, aseasonally reproducing sharks. The individual-adjusted AAFB method described here provides a simple way of improving estimates of life history parameters. It is especially easy to incorporate if back-calculation has been done, as no further measurements are needed to determine the FGI distribution. This method is applicable to any aseasonally reproducing chondrichthyan species, but may be particularly useful for small, fast growing, tropical carcharhinids e.g. *Carcharhinus dussumieri*, *Loxodon macrorhinus*, *Rhizoprionodon porosus*, *Scoliodon laticaudus* (Teshima and Mizue, 1972; Teshima *et al.*, 1978; Stevens and McLoughlin, 1991; Mattos *et al.*, 2001). Use of a fixed value for AAFB also provided acceptable results, however the AAFB must be adjusted to 0.5 years to account for the fact that there is no mean-birth date for the population. Leaving the AAFB unadjusted in the present study led to greatly different projections of growth and maturity for this species. This highlights the importance of considering the appropriate AAFB in all chondrichthyan growth studies, irrespective of reproductive seasonality (Campana, 2001).

In the present study, the unadjusted AAFB analysis suggested that *R. acutus* has a moderate growth rate throughout its life, with an absence of a distinct asymptote. Such growth patterns are characteristic of larger, long-lived, species e.g. *Carcharhinus obscurus*, *Carcharhinus brachyurus* (Walter and Ebert, 1991; Simpfendorfer *et al.*, 2002b) and are unlikely to be reflective of true growth for *R. acutus*. Adjusting the AAFB to a value of 0.5 years indicated rapid growth to asymptotic size early in life, characteristic of other growth studies on *Rhizoprionodon* spp. (Parsons, 1985; Branstetter, 1987a; Simpfendorfer, 1993; Carlson and Baremore, 2003; Loefer and Sedberry, 2003). However, asymptotic sizes reached using mean-adjusted AAFB were unrealistically small relative to the larger observed lengths within the collected sample. Using the individual-adjusted AAFB increased asymptotic size and also produced biologically realistic estimates of growth for this species. As such, we believe the individual-adjusted method was most appropriate for determining growth in *R. acutus* and represented a substantial improvement over the other two methods.

The individual adjustments we made to AAFB were based on the FGI distribution and were not truly reflective of growth. This is illustrated by the gaps between different age classes, most evident in males (Figure 3.5). We attributed the gaps to (i) measurement error, and (ii) opaque

(winter) bands that formed soon after birth being inseparable from the birth mark for some period of time. As such, very small values of FGI could not be measured, leading to a slight truncation of the FGI distribution. If the values used for FGI_{MAX} were a true representation of maximum growth in a year then we would expect a continuous distribution between the different age classes.

Individual-adjusted growth rates of *R. acutus* in the present study were consistent with congeneric species. Estimates of von Bertalanffy growth parameter, K , were 0.63 for females and 0.94 for males. Growth rates of *R. acutus* were slower than that of the smaller *Rhizoprionodon taylori* ($K= 1.0-1.3 \text{ yr}^{-1}$) (Simpfendorfer, 1993) and within or above the range of values found for the larger *Rhizoprionodon terraenovae* ($K= 0.359-0.850 \text{ yr}^{-1}$) (Parsons, 1985; Branstetter, 1987a; Carlson and Baremore, 2003; Loefer and Sedberry, 2003). Estimates of age at maturity and longevity were also concordant with the above studies. Size at maturity estimates were close to those estimated for *R. acutus* by Stevens and McLoughlin (1991) who found that both sexes mature at around 750mm.

Two previous studies have investigated growth rates of *R. acutus* in the waters of India. Krishnamoorthi and Jagadis (1986) obtained a value of 0.2 for K using Holden's (1974) method for predicting adult growth rate based on embryonic growth. Kasim (1991) also used size-mode-analysis and obtained K values of ~ 0.6 for both sexes. Both these studies substantially underestimated growth rates of *R. acutus*. This is not surprising however, as the first method is invalid (Pratt and Casey, 1990), and the second method used size-mode analysis which Simpfendorfer (1993) found to be poorly suited to *R. taylori* because of its growth characteristics. Growth parameters obtained in the present study are therefore the first rigorous estimates for this species and confirm that *R. acutus* grows fast and rapidly reaches maturity.

The information theoretic approach to modelling growth used in this study proved an effective method for considering the fit of multiple growth models within and among different analyses. We carried out model averaging on asymptotic size (L_{∞}), the parameter common to all models, and also calculated model average growth rate at birth (dL/dt_0) and maturity (dL/dt_{MAT}) (Katsanevakis, 2006; Thorson and Simpfendorfer, 2009). We propose the use of these three quantities in future growth studies, as they can be calculated for all models (as opposed to model specific parameters such as K , which only occurs in the VB models), they provide useful

information about growth at critical life stages, and all are easily interpretable, unambiguous measurements (e.g. mm.yr⁻¹).

In the present study, we verified using RMI that annual translucent band formation occurs during winter. The seasonal distribution of RMI values was typical of many tropical Carcharhiniformes (Santana and Lessa, 2004; Romine *et al.*, 2006; Piercy *et al.*, 2007) lacking the distinctive pattern more frequently seen in temperate species (Goldman and Musick, 2006). Okamura (2009) demonstrated to what extent variation in timing and duration of band formation can obscure patterns in verification. These factors probably contributed to the slightly ambiguous pattern observed in RMI values in this study. Although validation was not possible in the present study, Branstetter (1987) has previously validated annual growth band pair deposition for the congeneric species *Rhizoprionodon terraenovae*. All other validated growth studies from the family Carcharhinidae (except Brown and Gruber, 1988) have also suggested a pattern of annual growth band pair deposition (Davenport and Stevens, 1988; Simpfendorfer *et al.*, 2002b; McAuley *et al.*, 2006). Additionally, Simpfendorfer (1993) provided strong evidence to support annual growth band pairs for *R. taylori*. Although the evidence for annual growth band pair deposition is not clear-cut in the present study, there is strong evidence to support it at the genus and family level. This highlights the necessity of age validation studies (e.g. tag recapture, chemical marking) for tropical sharks where RMI analysis may not be particularly informative.

The results of this study suggest that *R. acutus* is a biologically productive species compared with many other chondrichthyans. In an analysis of 164 species of shark, (2000) found that sexual maturity occurred at approximately 75% of maximum size and 50% of maximum age for most sharks. In the present study both sexes reached maturity at ~80% of their maximum observed size and ~25% of maximum observed age. These life history characteristics suggest that *R. acutus* probably experience high levels of natural mortality which are balanced by maturing at a much smaller proportion of its maximum age. In north-eastern Australian waters, the reported commercial net catch of *R. acutus* is relatively low at present. Given its life history characteristics, this suggests that *R. acutus* is probably at a low risk of overexploitation. This needs to be confirmed by the collection of more detailed catch and effort data however. Levels of discarding from the penaeid targeting demersal trawl sector may also represent a significant source of mortality for *R. acutus* across northern Australia, as the implementation of bycatch reduction devices does not seem to have reduced catch of this species (Stobutzki *et al.*, 2002).

3.5 CONCLUSIONS

The aseasonal reproductive cycle displayed by many species of chondrichthyans can result in incorrect estimates of age when the traditional methods of ageing are used. For fast growing species in particular, the age at the first growth band pair needs to be corrected to account for this, otherwise erroneous estimates of growth rate will be obtained. We provide a simple method of making these corrections, and demonstrate how growth and maturity estimates can be improved using *R. acutus*, a small, tropical shark, as an example. The results of this study confirm that *R. acutus* grows rapidly and reaches maturity quickly. Despite its cosmopolitan distribution and importance to fisheries throughout its range, these are the first comprehensive estimates of age and growth for *R. acutus*. Given the high and likely increasing fishing pressure on this species throughout most of its range, this study will provide an important reference for countries where it is more heavily exploited.

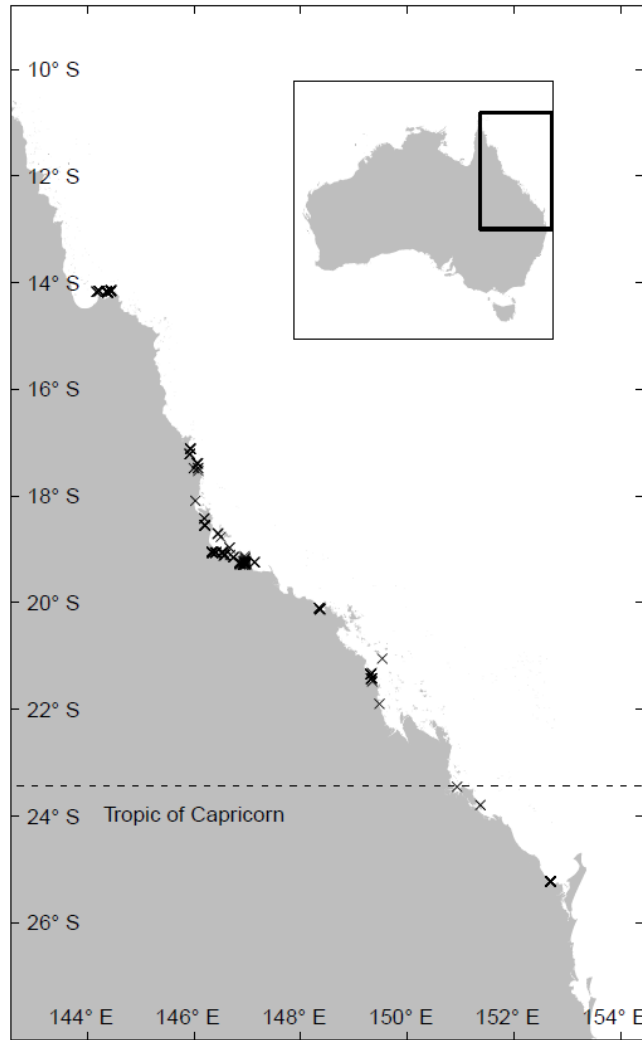


Figure 3.1 Map showing the study region. Sampling locations are denoted by crosses.

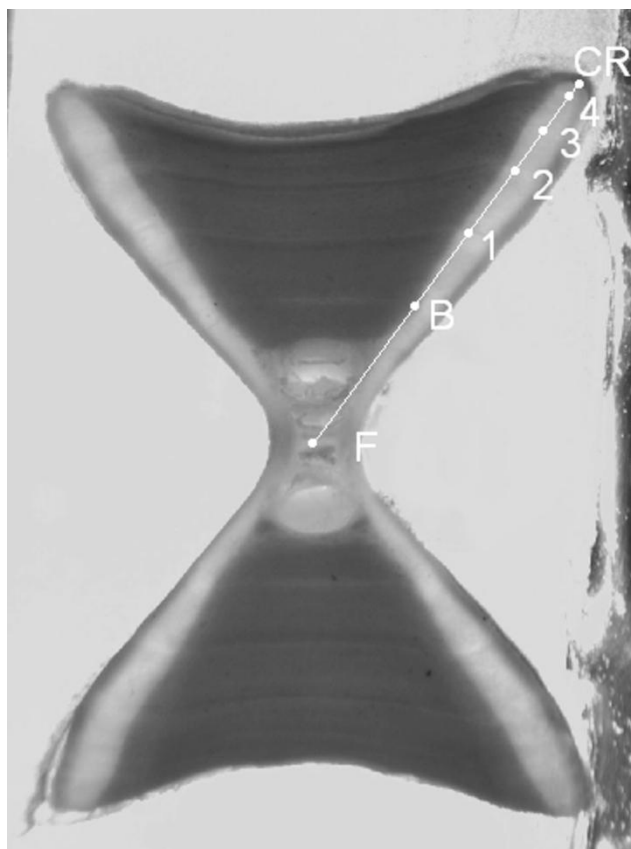


Figure 3.2 Sectioned vertebrae centrum from an 854 mm mature male *Rhizoprionodon acutus* with four growth band pairs visible. The white line is an example of a transect through the corpus calcareum used for back-calculation, showing the focus (F), birth-mark (B) and growth band-pairs (1-4). The centrum radius (CR) is the distance from F to CR. The distance from B to 1 is the first growth increment (FGI).

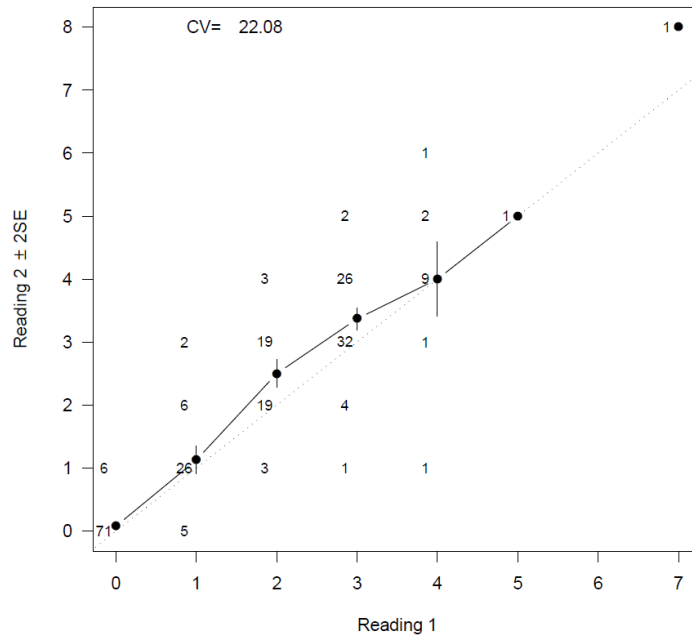


Figure 3.3 Age bias plot incorporating age-specific agreements between Reading 1 and 2 used for Bowker’s test of symmetry. Mean age-specific agreements ± 2 standard errors are plotted along with the 1-1 equivalence line for comparison. The coefficient of variation between reads was 22.08%.

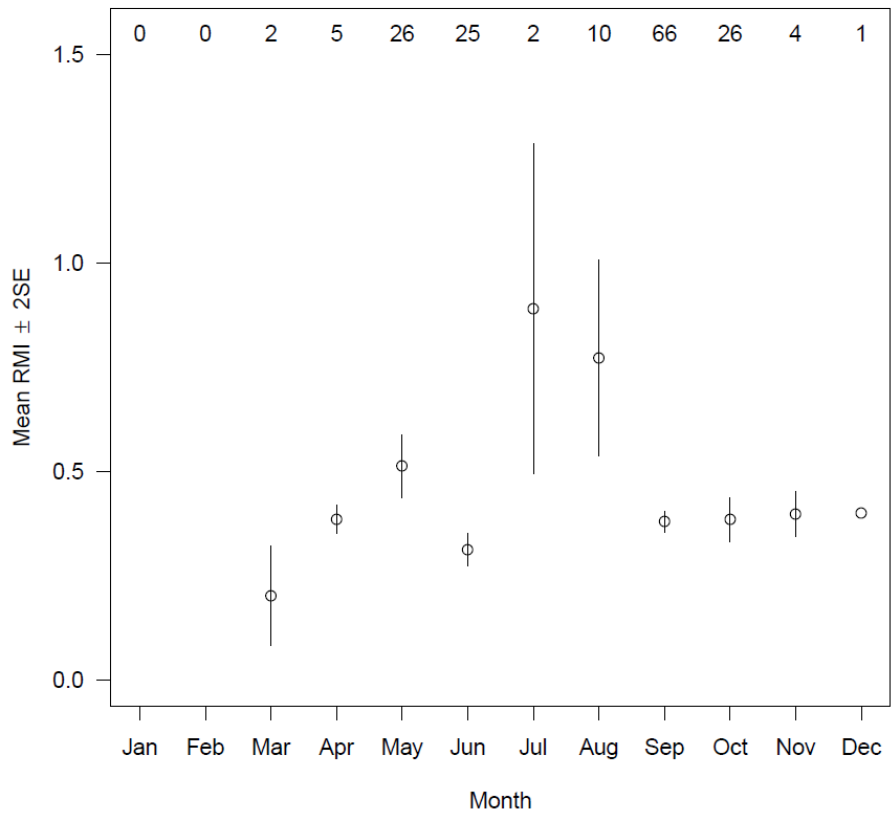


Figure 3.4 Mean relative marginal increment (RMI) ± 2 standard errors. Sample size for each month is shown at the top of the graph

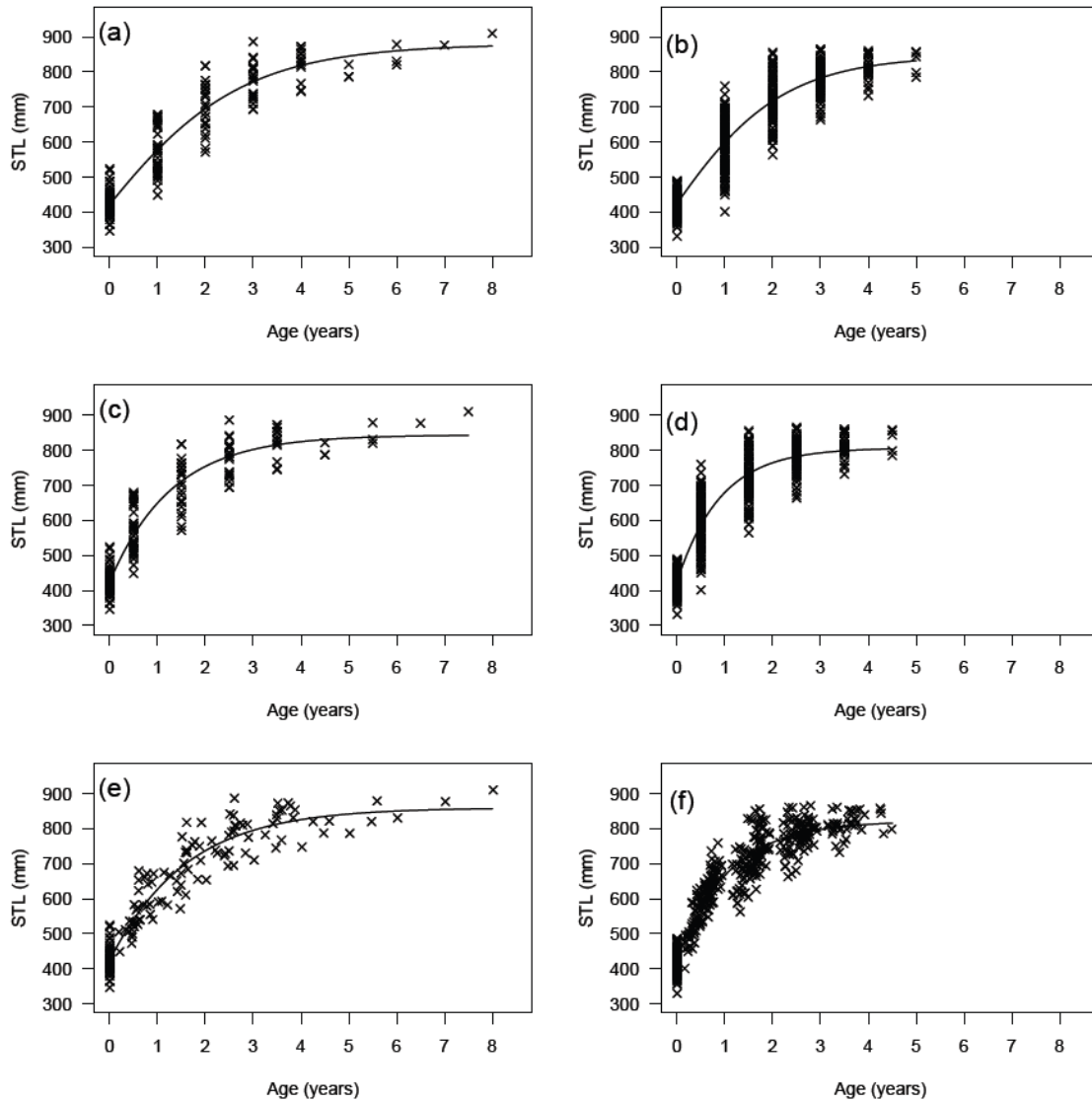


Figure 3.5 Growth analysis using back-calculated data for 71 female (n=196), and 160 male (n=507) *Rhizoprionodon acutus*. Points are size-at-age data with an unadjusted AAFB for females (a) and males (b), a mean adjusted AAFB (c) and (d) and individual-adjusted AAFB (e) and (f). Curves are model-averaged estimates of growth from 5 growth models fit to size-at-age datasets and weighted using AIC values.

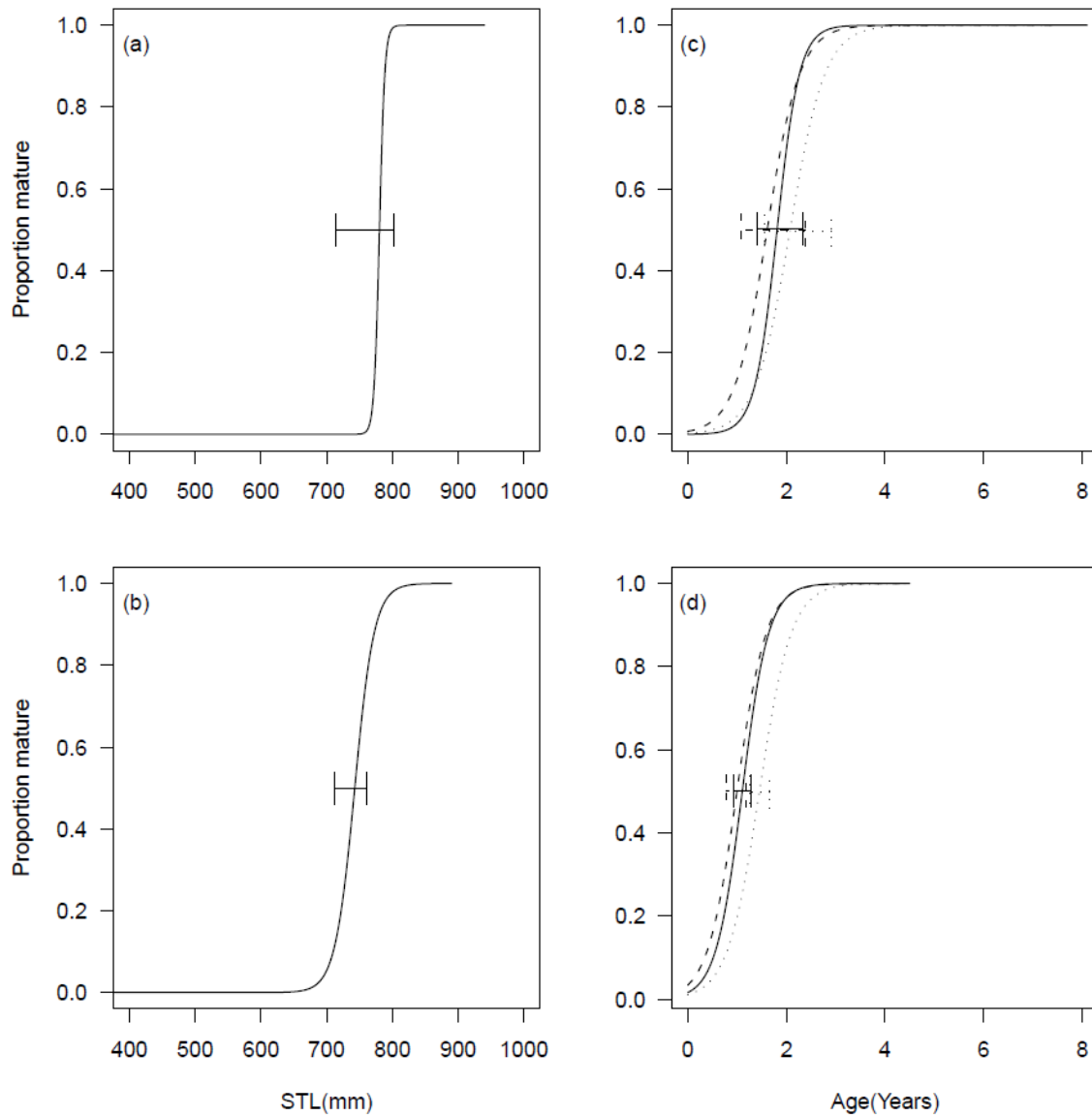


Figure 3.6 Length and age at maturity ogives fitted to maturity stage data for females: (a) and (c), and males: (b) and (d). Curves in (c) and (d) are results from different methods used to analyse growth: unadjusted (····), mean adjusted (---) and individual-adjusted (—) analyses. Brackets (slightly offset for age) are 95% bootstrap confidence intervals of the $L_{0.5}$ and $A_{0.5}$ estimates. Estimates of length and age at 50% maturity ($\pm 95\%$ CI) are:

	Length (mm)			Age (yrs)						
	$L_{0.5}$	(95%CI)	n	Unadjusted Age		Mean adjusted		Individual adjusted		
	$L_{0.5}$	(95%CI)	n	$A_{0.5}$	(95%CI)	$A_{0.5}$	(95%CI)	$A_{0.5}$	(95%CI)	n
Female	780	714-802	62	2.1	1.6-2.9	1.6	1.1-2.4	1.8	1.4-2.3	59
Male	742	716-762	176	1.5	1.3-1.7	1	0.8-1.2	1.1	0.9-1.3	153

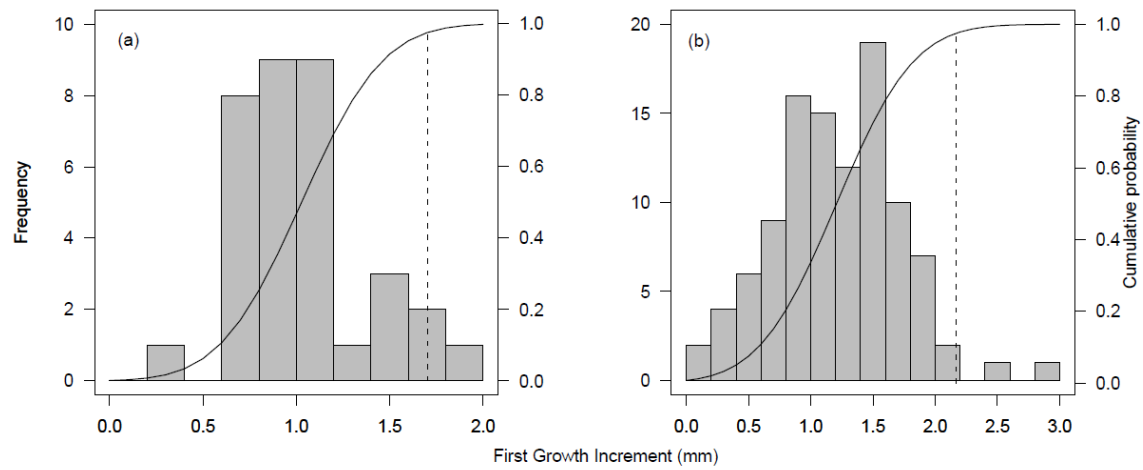


Figure 3.7 Histograms of back-calculated first growth increment (mm) for (a) females and (b) males. Solid lines are cumulative normal distributions. Dashed lines indicate the 97.5th percentiles of the normal distribution. This value was taken as the upper limit for first year growth.

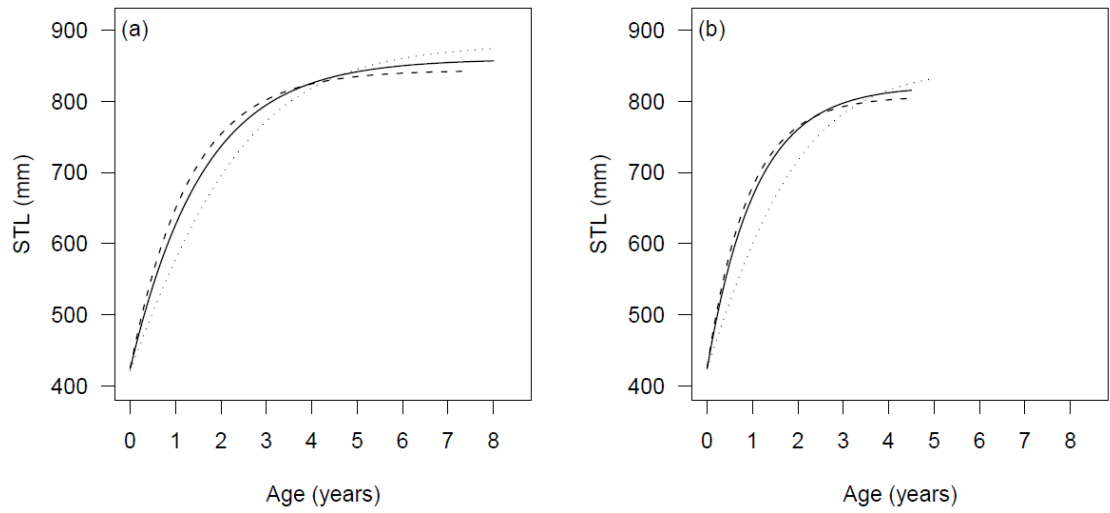


Figure 3.8 Comparison of the three model-averaged growth curves for (a) female and (b) male *Rhizoprionodon acutus*. Curves are unadjusted (····), mean-adjusted (---), and individual-adjusted (—) methods of analysing growth.

Table 3.1 Set of growth models used for multi-model inference, following Thorson and Simpfendorfer (2009)

	Model	Parameters	Growth function
g ₁	von Bertalanffy 3 (VB3)	3	$L(t) = \beta_2 + (\beta_1 - \beta_2)(1 - \exp(-\beta_3 t))$
g ₂	von Bertalanffy 2 (VB2)	2	$L(t) = L_0 + (\beta_1 - L_0)(1 - \exp(-\beta_2 t))$
g ₃	Gompertz	3	$L(t) = \beta_1 \exp(-\beta_2 \exp(-\beta_3 t))$
g ₄	Logistic	3	$L(t) = \frac{\beta_1 \beta_2 \exp(\beta_3 t)}{\beta_1 + \beta_2 (\exp(\beta_3 t) - 1)}$
g ₅	Schnute	4	$L(t) = \beta_1 (1 - (\beta_2 \exp(-\beta_3 t))^{\beta_4})$

Table 3.2 Results of the multi-model inference analysis of growth using three different values for the age at first band (AAFB). The performance of candidate models is ranked based on their AIC_c values. k is the total number of estimated parameters plus 1 for variance, Δ is the Akaike difference, and $w\%$ is the percentage Akaike weight.

Model	k	Adj.- R^2	AIC_c	Δ	$w\%$	Asymptotic length (mm)				Growth rate (mm/yr)	
						β_1	S.E.	95% Upper CI	95% Lower CI	dL/dt_0	dL/dt_{MAT}
Female Unadjusted											
Logistic	4	0.91	1351	0.0	50.0	866	15.91	897	834	158	97
Gompertz	4	0.91	1353	1.4	24.3	885	19.43	924	847	175	92
VB2	3	0.91	1354	2.9	11.7	919	26.49	971	867	196	86
Schnute	5	0.91	1355	3.6	8.3	886	33.55	952	820	176	92
VB3	4	0.90	1356	4.3	5.7	915	26.10	967	864	198	87
Model Average						881	26.61	934	829	171	93
Female Mean Adjusted											
VB2	3	0.91	1353	0.0	71.2	844	13.84	871	817	321	94
VB3	4	0.91	1355	2.1	25.0	844	14.14	872	816	321	93
Gompertz	4	0.90	1359	6.6	2.7	831	12.19	855	807	281	97
Schnute	5	0.90	1361	8.6	1.0	831	16.99	865	798	282	97
Logistic	4	0.90	1365	11.8	0.2	822	5.52	833	811	251	101
Model Average						844	14.10	871	816	319	94
Female Individual Adjusted											
VB2	3	0.93	1303	0.0	62.1	862	14.18	890	834	274	88
VB3	4	0.93	1305	1.9	23.6	861	14.26	889	833	275	88
Gompertz	4	0.93	1307	3.8	9.3	846	11.93	869	822	240	93
Schnute	5	0.93	1309	5.9	3.3	846	17.46	880	812	241	93
Logistic	4	0.93	1310	7.2	1.7	835	10.55	856	814	215	97
Model Average						859	15.23	889	829	269	89
Male Unadjusted											
Logistic	4	0.88	4015	0.0	57.8	836	9.33	855	818	185	124
Gompertz	4	0.88	4017	1.9	22.6	855	11.73	878	832	204	117
VB2	3	0.88	4019	3.8	8.4	886	15.95	917	854	227	111
Schnute	5	0.88	4019	3.9	8.1	855	25.60	906	805	204	117
VB3	4	0.88	4021	5.8	3.2	885	16.22	917	853	227	111
Model Average						848	18.59	884	811	196	120
Male Mean Adjusted											
VB2	3	0.88	4027	0.0	66.9	806	6.87	820	793	415	140
VB3	4	0.88	4029	1.4	32.9	808	7.11	821	794	411	139
Gompertz	4	0.88	4039	12.1	0.2	797	6.12	809	785	366	146
Schnute	5	0.88	4041	14.0	0.1	797	8.96	815	780	366	146
Logistic	4	0.88	4052	24.6	0.0	789	5.52	800	778	332	153
Model Average						807	6.98	820	793	414	140
Male Individual Adjusted											
VB2	3	0.93	3771	0.0	71.8	821	6.33	834	809	373	131
VB3	4	0.93	3773	1.9	28.1	821	6.40	833	808	375	131
Gompertz	4	0.93	3784	13.4	0.1	809	5.39	819	798	330	139
Logistic	4	0.93	3800	28.8	0.0	800	4.79	809	790	296	146
Schnute	5	0.93	3786	15.2	0.0	809	8.24	825	793	330	139
Model Average						821	6.36	834	809	374	131

Table 3.3 Best fit parameter estimates for all models in each analysis of growth. Corresponding parameters are found in Table 3.1.

Model	Sex	Unadjusted				Mean adjusted				Individual adjusted			
		β_1	β_2	β_3	β_4	β_1	β_2	β_3	β_4	β_1	β_2	β_3	β_4
	Female												
VB3		915.50	420.14	0.40		844.24	425.43	0.77		861.15	423.02	0.63	
VB2		919.14	0.39			843.93	0.77			862.14	0.62		
Gompertz		885.30	0.74	0.56		831.25	0.67	0.99		845.70	0.69	0.82	
Logistic		865.77	421.69	0.73		822.19	429.27	1.23		834.81	425.92	1.03	
Schnute		885.72	0.01	0.56	96.25	831.35	0.01	0.99	82.80	846.03	0.01	0.82	65.89
	Male												
VB3		884.76	423.87	0.49		807.51	428.26	1.08		820.78	423.76	0.94	
VB2		885.53	0.49			806.34	1.10			821.35	0.94		
Gompertz		855.26	0.70	0.68		797.08	0.62	1.38		808.73	0.64	1.21	
Logistic		836.26	424.96	0.89		789.10	431.18	1.70		799.89	426.92	1.49	
Schnute		855.29	0.01	0.68	131.74	797.22	0.01	1.37	68.45	808.81	0.01	1.20	59.67

**Chapter 4. The life history of Endangered hammerhead sharks
(Carcharhiniformes, Sphyrnidae) from the east coast of Australia**



Plate 4. Hammerhead sharks, *Sphyrna mokarran* (top and centre) and *Sphyrna lewini* (below), caught in Bowling Green Bay (September 2007).

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4.1 INTRODUCTION

The scalloped hammerhead, *Sphyrna lewini* (Griffith & Smith, 1834) and great hammerhead, *Sphyrna mokarran* (Rüppell, 1837) are two species of large, coastal-pelagic, semi-oceanic sharks found in tropical and warm temperate waters circumglobally (Compagno *et al.*, 2005). Both are a target or bycatch species in a wide variety of fisheries throughout their range and substantial population declines are suspected to have occurred in many areas as a result of fishing (Dudley and Simpfendorfer, 2006; Ferretti *et al.*, 2008; de Jong, 2009; Hayes *et al.*, 2009). Clarke *et al.* (2006) estimated that fins from hammerheads *S. lewini*, *S. mokarran* and *S. zygaena* made up around 6% of the Hong Kong shark fin trade. The ongoing demand for hammerhead fins, which are amongst the most highly valued of all shark fins, suggests that depletion is likely to continue at current levels of fishing. This inference is supported by an 80% increase in global reported catch of hammerheads between 2000 and 2007 (Lack and Sant, 2009). Consequently, both *S. lewini* and *S. mokarran* have been assessed as Endangered by the International Union for the Conservation of Nature (IUCN) (Baum *et al.*, 2007; Denham *et al.*, 2007).

In Australian waters, *S. lewini* and *S. mokarran* are considered to be less affected by fisheries than in other parts of the world and were assessed as Least Concern in a regional IUCN assessment (Cavanagh *et al.*, 2003). However, there are few long-term indices of hammerhead abundance in Australian waters, so this should be viewed cautiously. Indeed, Australian stocks are subject to similar fishing pressures as those in other parts of the world. On the east coast of Australia for example, *S. lewini* and *S. mokarran* make up around 7% and 10% of the biomass of elasmobranchs caught in small-mesh, inshore, gillnet fisheries in the Great Barrier Reef World Heritage Area (GBRWHA) (Chapter 2). Both are also killed in bather protection programs at metropolitan beaches along the coast using drum-lines and large-mesh gillnets (Dudley, 1997). A mid-shelf, demersal, longline fishery targets adults and subadults of these species south of the GBRWHA (Macbeth *et al.*, 2009), and a small number of hammerheads (probably *S. lewini* and *S. mokarran*) are also caught by pelagic longline fisheries operating offshore (AFMA, 2008). Trawl and recreational fisheries also affect these species to some extent throughout their range on the east coast of Australia. Fishing pressures across other parts of northern Australia are similar to those on the east coast (Bensley *et al.*, 2010) while an unknown but potentially high level of illegal unreported unregulated (IUU) fishing for sharks also occurs in waters off northern Australia (Lack and Sant, 2008; Field *et al.*, 2009).

As with many elasmobranch species, Australian and global management of *S. lewini* and *S. mokarran* stocks suffer from a critical lack of life history data that is necessary for informed and effective management of these species. The wide distribution of *S. lewini* and its large contribution to a range of fisheries has led to numerous studies of its life history (Stevens and Lyle, 1989; Chen *et al.*, 1990; Hazin *et al.*, 2001; Tolentino and Mendoza, 2001; de Bruyn *et al.*, 2005; Piercy *et al.*, 2007; White *et al.*, 2008). Despite extensive study, life history information available for *S. lewini* is still fragmentary. This may be partly due to the complex patterns of spatial organisation and migration of this species. Indeed few studies have been able to obtain adequate samples from all components of the population, with adult females, adult males and juveniles often residing in different areas (Klimley, 1987; White *et al.*, 2008). Studies of growth rates for *S. lewini* in particular are confounded by a number of factors including likely methodological differences, a lack of validation, and/or intraspecific differences between populations (e.g. Branstetter, 1987b; Chen *et al.*, 1990; Tolentino and Mendoza, 2001; Piercy *et al.*, 2007). In the case of *S. mokarran* its particularly large size and inherently low abundance in most areas has resulted in few studies of the life history of this species, and the first estimates of growth rates have only recently become available (Piercy *et al.*, 2010). Given the ongoing exploitation of these species throughout the world and especially in the Asia-Pacific region, along with the urgent requirement for life history data to inform fisheries managers, this study examined the age, growth and maturity of *S. lewini* and *S. mokarran* in eastern Australian waters. In addition to providing a general growth model for *S. lewini* off eastern Australia, this study also examined apparent spatial differences in growth and maturity of males between tropic and temperate waters.

4.2 METHODS

4.2.1 Sample collection

Biological samples were collected between December 2005 and May 2010 from a number of fishery-dependent sources along the east coast of Australia from Princess Charlotte Bay, Queensland (13°54'S) to the waters off Laurieton, New South Wales (31°36'S)(Figure 4.1). The majority of samples were obtained from a fishery observer program monitoring the commercial gillnet sector of the Queensland East Coast Inshore Finfish Fishery (ECIFF) (Chapter 2), in

shallow waters to 25m depth. Additional fishery-dependent samples were sourced opportunistically from: the Queensland East Coast Otter Trawl Fishery (unknown depth); mid-shelf, demersal longline fisheries operating in both Queensland and New South Wales waters (30-110m depth) (Macbeth *et al.*, 2009); and the Queensland Shark Control Program. Shark length was measured as stretched total length (L_{ST}) in millimetres (mm) following Compagno (1984): the animal was placed ventral side down and the upper lobe of the caudal fin was depressed in line with the body axis. Additional measurements of fork (L_F), and pre-caudal (L_{PC}) length were recorded for a subsample of animals.

4.2.2 Vertebral processing and growth analysis

A section of five vertebrae was removed from the anterior region of the vertebral column between the gills and the first dorsal fin and stored frozen. A scalpel was used to remove the neural and haemal arches and soft tissue leaving only the vertebral centra. Centra were then soaked in a solution of 5% sodium hypochlorite (bleach) for approximately 30 minutes to remove remaining tissue, then rinsed thoroughly under tap water, and placed in a drying oven at 60° C for 24 hours. One of the five centra prepared from each individual was selected for ageing. A single 400 – 600 µm longitudinal section was taken through the focus of the centrum using a slow-speed saw with a diamond-tipped blade (Beuhler, Illinois, USA) (Cailliet and Goldman, 2004). Centra < 10 mm in diameter were cast in a clear polyester resin prior to sectioning as they were too small to fit in the vice of the saw. The vertebrae section was fixed to a glass slide using Crystal Bond adhesive (SPI Supplies, Pennsylvania, USA).

Sectioned centra were examined under a dissecting microscope using transmitted light and the age of an animal was determined by counting the pairs of opaque and translucent (hyper- and hypomineralised) growth bands deposited on the corpus calcareum (Cailliet and Goldman, 2004) (Figure 4.2). The birth mark (age 0) was identifiable by a change of angle on the corpus calcareum (Figure 4.2). For *S. mokarran*, which has a well-defined, seasonal reproductive cycle (Stevens and Lyle, 1989), partial ages were assigned using a mean population birth date of 1 November (see Chapter 4.3.7). Data from the present study suggested that *S. lewini* pups were being born throughout the year, so partial ages could not be assigned for this species although neonates with unhealed umbilical scars were given an age of zero. Prior to ageing all centra, a random sub-sample of 50 individuals was read by two readers to ensure that a consensus was reached regarding interpretation of the banding pattern. Inter-reader precision was evaluated

using Chang's (1982) method of the coefficient of variation (CV) and percent agreement following the method of Goldman and Musick (2006). Inter-reader bias was evaluated statistically using Bowker's test of symmetry (Evans and Hoenig, 1998). A single reader then aged each vertebrae twice. Intra-reader precision and bias was evaluated as described for two readers above.

A multi-model inference (MMI) information theoretic approach was used to determine the most appropriate growth model for each species (Burnham and Anderson, 2001; Katsanevakis and Maravelias, 2008). Following Thorson and Simpfendorfer (2009), an *a priori* set of five candidate models was fit to the length-at-age data, with each model representing an alternative hypothesis for growth (Katsanevakis, 2006). The candidate set consisted of a three-parameter version of the von Bertalanffy growth model (VB3), $L(t) = L_0 + (L_{\infty} - L_0)(1 - \exp(-kt))$ where $L(t)$ is length-at-age t and L_0 (length-at-birth), L_{∞} (asymptotic length), and k (growth completion rate) are fitted parameters. A two-parameter version of the von Bertalanffy growth model with a fixed length-at-birth for each species was also used (VB2). In the VB2 model, L_0 was fixed at 525 mm L_{ST} for *S. lewini* and 700 mm L_{ST} for *S. mokarran* (see Chapter 4.3.7). The three-parameter Gompertz model was given by the equation $L(t) = L_{\infty} \exp(-l \exp(-kt))$, where L_{∞} , λ and k are estimated parameters. The three-parameter logistic growth was given by the equation

$$L(t) = \frac{L_{\infty} / \exp(kt)}{L_{\infty} + l (\exp(kt) - 1)}, \text{ where } L_{\infty}, \lambda \text{ and } k \text{ are estimated parameters. Finally the four-}$$

parameter Schnute model was given by the equation $L(t) = L_{\infty} (1 - (l \exp(-kt))^{\gamma})^{\gamma}$, where L_{∞} , λ , k and γ are estimated parameters. Although the parameter L_{∞} is common to all models, all other parameters are not directly comparable among models.

Models were fitted using the method of nonlinear least squares in the statistical package R (R Development Core Team, 2009) and model performance evaluated using Akaike's Information Criteria (AIC). Because of the relatively small sample sizes in the present study, the small-

sample, bias-adjusted form of AIC was calculated as $AIC_c = AIC + \frac{2K(K+1)}{n-K-1}$, where K is the

total number of estimated parameters + 1 for variance (σ^2), n is the sample size, and AIC

$= n \log(S^2) + 2K$. The best model was the one with the lowest AIC_c value, AIC_{min} . AIC

differences were calculated as $\Delta_i = AIC_{c,i} - AIC_{min}$, and used to rank the support of the remaining models ($i = 1 - 5$) relative to the best model. Models with Δ of 0 - 2 had substantial support,

while models with Δ of 4 – 7 had considerably less support and models with $\Delta > 10$ had essentially no support (Burnham and Anderson, 2002). Akaike weights (w_i), were calculated as the weight of evidence in favour of a model being the best model in the set of candidate models (Burnham and Anderson, 2002). Ninety-five percent confidence intervals around the best-fit parameter estimates were derived from 10,000 re-sampled datasets using the bias-corrected accelerated bootstrap method (Efron and Tibshirani, 1993).

4.2.3 Spatial variation in growth of male *S. lewini*

The spatial extent of the study area was large (~18° of latitude) and differences in the biology of *S. lewini* were apparent between northern and southern samples (Figure 4.1). However, these were confounded by gear selectivity; northern samples were mainly collected from a small-mesh, inshore, gillnet fishery, while southern samples were mainly collected from a mid-shelf, demersal longline fishery. Further confounding the analysis of growth was the poorly documented spatial ecology of this species. For example, females > 1000 mm L_{ST} and males > 2000 mm L_{ST} were almost entirely absent from northern regions yet present in southern regions. It was unclear if this was due to a southerly migration of larger animals or related to other factors such as gear type, depth, temperature or habitat characteristics. Given the limitations of the sampling, which was opportunistic, it was not possible to fully reconcile these issues. However, for males there were sufficient data available to investigate potential spatial effects on growth between northern and southern regions.

Analysis of growth data proceeded as follows: a general growth model of *S. lewini* was first established using data pooled for both sexes and from all regions along the coast. A second analysis was then undertaken on males only to examine potential spatial effects on growth, where region was included as a two-level term: tropical and temperate. Samples were separated into the two nominal regions by the Tropic of Capricorn (23°26'S) (Figure 4.1). Following Kimura (1980), likelihood ratio tests were then used to statistically compare parameters between growth curves from each region. The most appropriate growth model used for the spatial comparison was determined from the initial MMI analysis with all samples pooled.

4.2.4 Age validation and verification

To validate the assumption that growth band pairs were deposited annually on the centra, a fishery-independent mark, tag and recapture study was carried out. Fishery-independent sampling using experimental multihook longlines was conducted between January 2008 and June 2010 in Cleveland Bay (19°12'S, 146°54'E) and Halifax Bay (19°6'S, 146°40'E) near Townsville in north Queensland. The length and sex of captured sharks were recorded and individuals were then tagged externally on the first dorsal fin using Rototags or Jumbotags (Dalton, Worldwide). The vertebral centra of captured sharks were marked using the fluorescent dye calcein (C₃₀H₂₆N₂O₁₃). A pH-buffered, isotonic solution of 12.5 mg.mL⁻¹ calcein was injected intramuscularly behind the first dorsal fin at a dosage of 5 mg.kg⁻¹ (McAuley *et al.*, 2006). The body weight of sharks was estimated using published length-weight relationships for these species off northern Australia (Stevens and Lyle, 1989).

The method of centrum edge analysis (CEA) described by Okamura and Semba (2009) was used as an additional tool to statistically verify the timing and frequency of translucent growth band deposition on vertebral centra. During age determination the centrum edge of each vertebra classed as either opaque or translucent. The monthly proportion of centra with opaque edges was then fitted to three models corresponding to hypotheses that opaque band formation occurs on an annual cycle, on a biannual cycle or without a cycle. The best-fit model was the one with the lowest AIC_c value. Given the relatively low sample sizes, both sexes and all age classes were pooled. Age 0 animals were excluded from the analysis because they lacked any fully formed band pairs, while individuals >2500 mm were also excluded because the band pairs were tightly spaced in those older animals.

4.2.5 Duration of first growth increment

In addition to validating the frequency of growth band pairs throughout life, establishing the duration of the first growth increment (and therefore the age of individuals when the first growth band pair is formed) is an important consideration in age and growth studies (Campana, 2001) (Chapter 3). To establish the duration of the first growth increment, the occurrence and length of age 0 animals and neonates throughout the year was examined using a plot of month against L_{ST} .

4.2.6 Maturity and reproduction

Reproductive staging of animals was determined based on the descriptions of Walker (2005). Maturity in males was determined by examining the claspers: stage 1 (immature), claspers pliable with no calcification; stage 2 (immature), claspers partly calcified; stage 3 (mature), claspers fully calcified. Female maturity was determined by visual examination of the uterus: stage 1 (immature), uniformly thin tubular structure; stage 2 (immature), thin tubular structure partly enlarged posteriorly; stage 3 (mature) uniformly enlarged tubular structure; stage 4 (mature), in utero eggs present without macroscopically visible embryos present; stage 5 (mature), in utero embryos macroscopically visible; stage 6 (mature), enlarged tubular structure distended. Maturity stage data was converted into binary form for statistical analysis (immature = 0, mature = 1).

Population estimates of length- and age-at-maturity were established using logistic regression analysis (Walker, 2005b). Length (L_{ST}) and age were modelled separately as a function of maturity stage (logit transformed) using generalised linear models (GLMs). For male *S. lewini* there were sufficient data to examine potential spatial effects on maturity by incorporating region and the interaction of region as terms in the GLM analysis. Region was a term with two levels (tropical and temperate) as used above in the spatial analysis of growth. For *S. mokarran* the effect and interaction of sex on maturity was examined by including sex as a term the GLM analysis. The effect of terms and interactions were examined and the most parsimonious model was the one with the lowest AIC. The small-sample, bias-corrected variation of AIC (AIC_c) was used following Burnham and Anderson (2002). Ninety-five percent confidence intervals of the best-fit parameter estimates and population estimates of length- (L_{ST}) and age-at-50%-maturity (L_{ST50} , A_{50}) were derived from 10,000 re-sampled datasets using the bias-corrected accelerated bootstrap method (Efron and Tibshirani, 1993).

4.3 RESULTS

4.3.1 Sample collection and length equations

Length measurements were obtained from a total of 522 *S. lewini* comprised of 324 males (465 – 2898 mm L_{ST}), 195 females (465 – 2600 mm L_{ST}) (Figure 4.3 a) and three animals of unknown sex (530, 600 and 700 mm L_{ST}). The majority of samples were obtained in the tropics ($n = 432$, Figure 4.1) via the ECIFF, where catches were composed mainly of neonates and juveniles of

both sexes and small adult males up to ~2000 mm L_{ST} . Larger adult males (up to 2900 mm L_{ST}) and juvenile females (1500 – 2000 mm L_{ST}) were predominantly encountered in the demersal longline fishery in temperate waters. Forty-one individuals were tagged, marked with calcein and released using fishery-independent sampling methods. These individuals were mainly small adult males 1400 – 2000 mm L_{ST} . The relationships between L_{ST} , L_F and L_{PC} for *S. lewini* (sexes combined) were

$$L_{ST} = 15.38 + 1.30 \cdot L_F \quad (r^2 = 0.99, p < 0.001, \text{d.f.} = 372)$$

$$L_{ST} = 15.49 + 1.43 \cdot L_{PC} \quad (r^2 = 0.99, p < 0.001, \text{d.f.} = 250).$$

Length measurements were obtained from 146 *S. mokarran* comprising 65 males (801 – 3693 mm L_{ST}), 77 females (795 – 4397 mm L_{ST}) (Figure 4.3 b) and four animals of unknown sex (890, 1100, 1210 and 1220 mm L_{ST}). The majority of samples were from the tropics ($n = 123$, Figure 4.1) and were obtained from the ECIFF. Tropical samples were biased toward females and included animals of all lengths except neonates, while the demersal longline fishery samples in temperate waters were mainly larger males (> 2000 mm L_{ST}). Thirty-eight individuals were tagged, marked with calcein and released during the study, and were mostly immature males (1600 – 2000 mm L_{ST}). The relationships between L_{ST} , L_F and L_{PC} for *S. mokarran* (sexes combined) were

$$L_{ST} = 49.01 + 1.29 \times L_F \quad (r^2 = 0.99, p < 0.001, \text{d.f.} = 98)$$

$$L_{ST} = 74.19 + 1.39 \times L_{PC} \quad (r^2 = 0.99, p < 0.001, \text{d.f.} = 50).$$

4.3.2 Validation of growth band pattern

Recapture rates of hammerheads tagged during fishery-independent sampling were high. Seven of the 41 marked *S. lewini* were recaptured including three on multiple occasions. All recaptures were considered to be too soon after the original tagging date, so the animals were re-released and as a result no calcein marked vertebrae were recovered from this species. Consequently, centrum edge analysis was used to verify the periodicity of band pair formation. Two hundred and thirty-three centra had at least one growth band pair and were therefore available for the analysis (Figure 4.4). Using the method proposed by Okamura and Semba (2009), AIC_c values were: 262.48 for the model of an annual cycle; 267.07 for the biannual cycle model; and 269.94 for the model hypothesising no cycle in opaque band formation. The greatest proportion of opaque bands occurred in November followed by December (Figure 4.4) but high

values also occurred during March and July. Although the annual model was statistically the best supported, computed AIC_c differences, Δ , were 4.59 and 7.46, implying that there was still some support for the models of a biannual cycle or no cycle. In the absence of a conclusively verified banding pattern for *S. lewini*, growth analysis proceeded with the assumption of an annual cycle. The implications of this are examined further in the discussion.

Five of the 38 calcein marked *S. mokarran* were recaptured after periods of between 126 and 467 days at liberty (Table 4.1). Vertebrae were recovered from all animals except GHH2, which was recaptured during fishery-independent sampling and re-released given the relatively short time at liberty. Two individuals, at liberty for 353 days and 467 days, had each formed a single opaque band after the calcein mark, supporting the hypothesis that band pairs are deposited annually on the vertebrae. The remaining two individuals, at liberty for 126 days and 186 days, had not formed any opaque bands. All three animals marked with calcein during October or November (GHH1, GHH3 and GHH4) had formed opaque bands closely preceding the calcein mark. Furthermore, animal GHH1, which was recaptured in November, had an opaque band formed on the outer margin of the centra. This suggests that opaque band formation in *S. mokarran* probably occurs during spring (October-November) in tropical eastern Australian waters.

4.3.3 Duration of first growth increment

No clear trends in the occurrence or lengths of age-zero *S. lewini* were observed during the year (Figure 4.5 a) and neonates were present throughout the year. For an aseasonally reproducing species, the mean age of the population when the first growth increment is formed should be 0.5 years (Chapter 3). However, high abundances of *S. lewini* neonates during November and December suggested reproduction was probably not completely aseasonal, but rather partially seasonal. Without more detailed knowledge on the timing of parturition, no adjustments could be made to the first growth increment, which was left at one year for all individuals.

Examining the occurrence and length of age-zero *S. mokarran* (Figure 4.5 b) showed a pattern concordant with a seasonally reproducing species. Although no neonates were captured, a pregnant female was captured in October with full-term embryos suggesting birth occurs around this time. Age validation suggested growth bands were formed at a similar time of the year, therefore making the first growth increment approximately one year in duration. The largest age-

zero individuals (850 – 950 mm L_{ST}) were captured between September and November, further supporting this (Figure 4.5 b).

4.3.4 Precision and bias in age estimation

Inter-reader mean percent agreement (PA) and $PA \pm 1$ year summed across 100 mm length groupings was 46% and 80.71% for *S. lewini*, while Chang's coefficient of variation (CV) was 17.9%. Bowker's test of symmetry indicated there was no systematic bias ($\chi^2 = 18.33$, d.f. = 12, $p = 0.106$, Figure 4.6 a). Intra-reader precision for *S. lewini* was similar; mean PA and $PA \pm 1$ year was 50% and 79%, while CV was 14.64%. There was no systematic intra-reader bias ($\chi^2 = 40.09$, d.f. = 31, $p = 0.127$, Figure 4.6 b). Measures of precision and age bias plots indicated *S. lewini* vertebrae could be accurately (~80% of the time) aged to within 1 year both between and among readers without bias (Figure 4.6 a – b).

For *S. mokarran* inter-reader measures of precision were somewhat lower (PA = 35%, $PA \pm 1$ yr = 64%, CV = 16.84%), although there was no systematic inter-reader bias ($\chi^2 = 15.33$, d.f. = 18, $p = 0.639$, Figure 4.6 c). Intra-reader precision for *S. mokarran* was considerably higher (PA = 48%, $PA \pm 1$ yr = 86%, CV = 17.23%), again with no systematic bias between reads ($\chi^2 = 21.67$, d.f. = 22, $p = 0.479$, Figure 4.6 d). Given that measures of precision were within the usual range for elasmobranch studies and there was no systematic bias (Figure 4.6 c – d), it was concluded that an acceptable and repeatable interpretation of the banding pattern had been achieved.

4.3.5 Growth analysis

Vertebral samples were obtained from a total of 392 *S. lewini*, comprising 230 males (465 – 2898 mm L_{ST}), 159 females (465 – 2600 mm L_{ST}) and three animals of unknown sex (540 – 700 mm L_{ST}). Male *S. lewini* reach at least 3010 mm L_{ST} in Australian waters (Stevens and Lyle, 1989) and vertebral samples close to this length were obtained. However, given females attain a length of at least 3460 mm L_{ST} in Australian waters and the largest sample obtained was 2600 mm L_{ST} , our samples were unlikely to provide a full representation of growth in females. The oldest male and female *S. lewini* aged in the present study were 21 years (2617 mm L_{ST}) and 15 years (2600 mm L_{ST}), respectively. In the initial growth analysis with data pooled between regions and sexes, the three-parameter von Bertalanffy (VB3) growth model had the greatest support and was considered most appropriate given the data (Table 4.2, Table 4.3, Figure 4.7 a). The AIC

differences (Δ) between the other candidate models were high (>10), indicating negligible support for those models.

Of the 230 male samples for which an age was determined, 200 were obtained from tropical regions and 30 from temperate regions (Figure 4.1). Male samples from temperate regions were larger (505 – 2898 mm L_{ST}) and older (0 – 21 years) than samples obtained from tropical regions (465 – 1970 mm L_{ST} , 0 – 12 years). Hypothesis testing for the effect of region on growth showed that there were significant differences between growth rate, k , and asymptotic length, L_{∞} , between tropical and temperate samples (Table 4.3, Table 4.4, Figure 4.7 b). However, there was no significant difference between length-at-birth, L_0 , between regions, and hence a single parameter was included in the most parsimonious model (Table 4.3). The relatively low sample size from temperate regions led to much higher uncertainty around parameter estimates compared to the tropics (Table 4.3). Despite this, comparison of approximate confidence intervals around k and L_{∞} parameters between regions highlighted the large differences in both growth rate and asymptotic length (Figure 4.7 c). Based on the model predictions, males from temperate regions grew approximately a metre larger and had a k value approximately half that of males in the tropics.

Vertebral samples were obtained from a total of 100 *S. mokarran*, comprising 43 males (801 – 3691 mm L_{ST}), 51 females (795 – 4391 mm L_{ST}), and six animals of unknown sex (890 – 1220 mm L_{ST}). The oldest male and female aged in the present study were 31.7 years (3691 mm L_{ST}) and 39.1 years (4391 mm L_{ST}), respectively. In the multimodel growth comparison computed AIC_c values were lowest for the VB2 model and so it was considered most appropriate given the data (Table 4.2, Table 4.3, Figure 4.7 d). The VB3 model was also supported by the data ($\Delta = 1.95$, $w = 0.2738$), however the VB2 was clearly preferable ($w = 0.7262$) as it reduced the number of parameters and had a similar explanatory power to the VB3 model (Table 4.2).

Growth rate parameters were similar between *S. lewini* and *S. mokarran* for the models with data pooled for regions and sex ($k = 0.077$ and 0.079 yr^{-1} , Table 4.3) and suggested the two species had similar growth characteristics: both were relatively long lived and slow growing. However, the regional comparison of growth in male *S. lewini* also indicated that within the overall population some components had considerable variation in their growth characteristics.

4.3.6 Maturity analysis

Length- and age-at-maturity data were available for 264 and 187 male *S. lewini* respectively (465 – 2898 mm L_{ST} and 0 – 21 years). The smallest mature male was 1288 mm L_{ST} (unknown age) while the youngest mature male was 3 years old (1320 mm L_{ST}); both were captured in the tropics. The largest immature male was 1989 mm L_{ST} (unknown age), while the oldest immature male was 9 years (1846 mm L_{ST}); both captured in temperate waters. Logistic regression analysis found that, like growth, region had a strong influence on length- and age-at-maturity (Table 4.5). However, the interaction between length or age and region did not improve the overall performance of the model enough to justify its inclusion. The removal of region altogether considerably decreased the explanatory power of the models and the models with the smallest AIC_c values for both length and age included region as a factor. A separate intercept was therefore fitted to account for this factor (Table 4.5, Table 4.6). Estimates of L_{ST50} and A_{50} (with 95% CI) for *S. lewini* males differed considerably between regions and occurred at 1471 (1423 – 1519) mm and 5.7 (5.1 – 6.2) years in the tropics and 2043 (1934 – 2182) mm and 8.9 (7.5 – 10.8) years in temperate waters (Figure 4.8 a – d). The relatively small sample sizes in temperate regions led to greater uncertainty in parameter estimates and this is reflected in the much larger 95% confidence intervals around L_{ST50} and A_{50} estimates compared with tropical samples. Although length- and age-at-maturity data were available for 100 and 93 female *S. lewini* respectively (469 – 2600 mm L_{ST} and 0-15 years), only a single mature female was obtained (2600 mm L_{ST} , 15 years). It was therefore not possible to statistically determine length or age at maturity of females. The largest and oldest immature female was 1982 mm L_{ST} and 12 years old. Two immature females of 1794 mm and 1859 mm L_{ST} were 10 and 9 years respectively.

For *S. mokarran* length- and age-at-maturity data were available for 59 and 42 males (801 – 3691 mm L_{ST} and 0.25 – 31.7 years) and 26 and 24 females (795 – 4280 mm L_{ST} and 0.4 – 34.6 years). The largest immature male and female were both 2420 mm L_{ST} and aged 7.5 years. The oldest immature male was 9.8 years (2100 mm L_{ST}), while the oldest immature female was 7.6 years (2030 mm L_{ST}). The smallest and youngest mature female was 2120 mm L_{ST} and 6.7 years old, while the smallest and youngest mature males were 2267 mm L_{ST} (10.2 years) and 8.6 years (2507 mm L_{ST}). The lengths and ages over which maturity occurred were variable and there was minimal difference between sexes in the range over which it occurred. Therefore, given the relatively low sample sizes, the most parsimonious models with the lowest values of AIC_c included neither sex nor the interaction between length or age and sex (Table 4.5, Table 4.6).

Consequently data for both sexes were pooled. For *S. mokarran* L_{ST50} occurred at 2279 (2149 – 2429) mm and A_{50} occurred at 8.3 (7.4 – 9.5) years (Table 4.6, Figure 4.8 e and f).

4.3.7 Notes on reproductive cycle and length-at-birth

Little could be observed directly on the reproductive cycle of either species due to the absence of adult female *S. lewini* in catches, and the apparent rarity of pregnant *S. mokarran*. Although some of the larger female *S. mokarran* may have been pregnant, the small-scale nature of the inshore net fishery and large size of these animals meant that dissection and examination of the uteri was rarely possible. One pregnant female (4280 mm L_{ST}) caught in the tropics (17°5'S) during May had 39 embryos (18F, 21M) with a mean length of 376 mm L_{ST} . A second pregnant female (3921 mm L_{ST}), caught in October in the tropics (19°5'S) had 21 full-term embryos. Lengths (L_{ST}) for two retained embryos were 705 mm (1.57kg) and 710 mm (1.59kg), the two largest recorded for this species. The single adult *S. lewini* (2600 mm L_{ST}) was recorded as pregnant with in utero eggs, however no additional measurements were recorded. Neonate *S. lewini* with open umbilical scars indicating recent birth were recorded in small numbers throughout the year as far south as Moreton Bay but were most abundant in late November and early December. Using those neonates, length-at-birth was inferred at between 465 and 563 mm L_{ST} (n = 55, Figure 4.5 a).

4.4 DISCUSSION

4.4.1 Life history of Sphyrna lewini

The results of this study increase our understanding of the complex life history of this widespread and formerly abundant large shark species that is important to fisheries throughout its range. The study indicated that off the east coast of Australia, neonates are born in shallow intertidal habitats throughout the year, however there appeared to be a peak in pupping during late spring and early summer (November – December). This suggests the reproductive cycle is likely to be partially aseasonal with a peak during summer. Stevens and Lyle (1989) found evidence of a similarly protracted pupping season in the Arafura Sea, while the data of White *et al.* (2008) suggest a seasonal reproductive cycle in the waters off Indonesia. The study also indicated that in the tropics many juveniles of both sexes remain in shallow inshore habitats <25m for the first few years of life, but by age 3 and ~1000 mm L_{ST} females are almost completely absent from this

depth range, presumably having migrated to deeper water. In contrast, many males up to age 10 and 2000 mm L_{ST} , including many sexually mature individuals, were sampled from those inshore waters. However, despite extensive fishery-dependent and -independent sampling, males >2000 mm were rarely encountered. Sexual segregation at some level is ubiquitous among chondrichthyans, and is particularly pronounced and well documented in *S. lewini* (Klimley, 1987; Sims, 2005).

The pronounced sex-segregation of *S. lewini* off the coast of Australia precluded detailed study of females, but revealed some striking insights into the life history of males. Length- and age-at-maturity in male *S. lewini* in eastern Australian waters was highly variable. In tropical waters within the inner lagoon of the Great Barrier Reef (GBR), 50 % of males were mature at 5.6 years old and 1471 mm L_{ST} , one of the smallest lengths reported globally, and concordant with the estimate of Stevens and Lyle (1989) off northern Australia (1400-1600 mm L_{ST}). Yet in more temperate waters south of the GBR and Tropic of Capricorn, males matured both larger ($L_{ST50} = 2043$ mm) and older (8.9 years) than in northern areas, as also was noted by Stevens (1984). Differences in maturity characteristics also extended to differences in growth: males from the tropics grew at a much faster rate and to a much smaller asymptotic length ($k = 0.163 \text{ yr}^{-1}$, $L_{\infty} = 2119$ mm L_{ST}) compared to those from temperate regions ($k = 0.093 \text{ yr}^{-1}$, $L_{\infty} = 3199$ mm L_{ST}).

Intuitively, the differences in maturity and growth characteristics observed in males would appear to be an effect of latitudinal differences within the wide spatial extent of the study area. Yet sampling for *S. lewini* occurred all along the coast, and in both regions maturation occurred within a discrete length and age range with no apparent overlap or gradient. Based on the relatively small sample size from temperate regions, coupled with the differences in gear type, it is also tempting to suggest that the observed differences in male biology were purely methodological. Yet there is evidence to support the notion that the observed differences in biology are, in fact, real.

It is well established that many life history variables are correlated and predicted by adult body size (Charnov, 1993). For example, the ratio of length-at-maturity to maximum length is invariant in many taxa, including fish (Frisk *et al.*, 2001). This can also be seen in hammerheads including *S. lewini* (Figure 4.9 a). It therefore follows that the difference in length-at-maturity of approximately 500 mm between tropic and temperate samples probably extends to differences in maximum length (and growth). The extensive length frequency data of male *S. lewini* ($n = 3852$)

presented by Stevens and Lyle (1989) were similar to this study and indicate that in tropical waters off northern Australia, male *S. lewini* $> 2100\text{mm } L_{ST}$ were rarely captured.

Overall, these findings suggest there is pronounced intra-specific dimorphism among male *S. lewini* in Australian waters. As differences were found between tropical and temperate samples this indicates temperature could be a driving factor, however the depth where the samples were collected also differed and this factor could be equally important. Irrespective of the cause, the finding points to the existence of two separate and non-mixing groups of male *S. lewini* in Australian waters. A search of the literature reveals that similar dimorphism of male *S. lewini* appears to occur in other parts of the world, although it appears to generally have been overlooked. For example Bass *et al.* (1975) found males matured within the range of 1400-1650 mm L_{ST} in southern Mozambique, much smaller than the L_{ST50} of 2160 mm (range 1825 –3061 mm L_{ST}) reported by de Bruyn *et al.* (2005) just south in Durban. Similarly in Brazil, Hazin *et al.* (2001) found males caught by pelagic drift-nets were mature at lengths > 2000 mm L_{ST} , while the observations of Lessa *et al.* (1998) suggest males on the coast matured at lengths <1500 mm L_{ST} . These studies suggest that dimorphism in length-at-maturity of *S. lewini* may be common.

Recent molecular work on samples from the present study suggest that males on the east coast of Queensland are likely to be composed of a single stock (Welch *et al.*, 2010). It is therefore hypothesised that two distinct male forms exist: coastal strategists and pelagic strategists. Although *S. lewini* are born in coastal habitats, it is well documented that females in particular migrate offshore soon after birth, possibly to exploit higher-energy pelagic prey (Klimley, 1987; Stevens and Lyle, 1989). Recent work suggest females may regularly inhabit the mesopelagic zone, using depths up to 1000 m (Jorgensen *et al.*, 2009). For *S. lewini* the necessary conditions of the female reproductive strategy are therefore both pelagic and coastal habitats. As reproduction is thought to be annual in *S. lewini* (Chen *et al.*, 1988; White *et al.*, 2008), this would imply at least annual migration between these habitats for an adult female *S. lewini*.

Males, on the other hand, do not have such strict requirements. While it appears all females disperse from their natal grounds, the occurrence of adult males offshore (Hazin *et al.*, 2001) and outside of known nursery grounds (de Bruyn *et al.*, 2005), as well as in nursery grounds (present study), indicates that some males disperse while others remain. It is hypothesised that the observed dimorphism represents a trade-off between reproductive success and reproductive opportunity, and that males form two distinct groups: pelagic strategists and coastal strategists.

Pelagic strategists are males that disperse from their natal grounds, migrating offshore like females, and also ranging further into temperate waters. Coastal strategists however, remain in inshore waters for their entire lives. Pelagic strategists attain a large maximum length (~3000 mm) that is close to that of females and therefore likely to be optimal for reproduction (Cortés, 2000). Coastal strategists however may gain an advantage by being able to opportunistically mate with females entering coastal waters to give birth, which has been postulated to occur directly after parturition (Clarke, 1971; Chen *et al.*, 1988). If coastal strategists faced less competition, they may be selected to mature at younger ages, potentially explaining their smaller size and lower longevity. Alternatively, their smaller size may be due to restrictions in prey availability in coastal areas. Studies into the spatial ecology of *S. lewini* are needed to further investigate this hypothesis. However it may potentially explain the dimorphism between males observed in some parts of the world, especially in areas such as northern Australia where there is a wide continental shelf and where a distance of hundreds or even thousands of kilometres separates female nursery grounds and suitable pelagic habitats.

Although males dominated the catch of Australia's coastal fisheries and hence growth models of this study, female growth was still represented in the general growth model (both sexes and regions) where vertebral ages were obtained from 159 females up to 2600 mm L_{ST} . Overall, growth rates of *S. lewini* based on the general model were within the range of previous studies. Yet hindering any meaningful comparisons of growth rates with other studies was the serious issue of age validation, which has yet to be conclusively resolved for this species. Consequently, all existing growth studies of *S. lewini* fall into two categories based on interpretation of the vertebral banding pattern: those assuming band pairs are formed annually, and those assuming band pairs are formed biannually.

Chen *et al.* (1990) first reported that growth band pairs were formed biannually in *S. lewini*. At the time, this hypothesis was supported by studies reporting biannual deposition of growth bands in *Isurus oxyrinchus* and *Cetorhinus maximus* (Parker and Stott, 1965; Pratt and Casey, 1983), both of which have since been disproved (Campana *et al.*, 2002; Natanson *et al.*, 2006; Natanson *et al.*, 2008; Semba *et al.*, 2009). Two subsequent studies of *S. lewini* growth in the eastern Pacific have also assumed biannual growth band deposition (Tolentino and Mendoza, 2001; Tolentino *et al.*, 2008). Conversely, two growth studies of *S. lewini* within the Atlantic have assumed annual growth band deposition (Branstetter, 1987b; Piercy *et al.*, 2007). Unfortunately

the prevailing feature of *S. lewini* growth studies is that all have used indirect methods to verify growth, and none has proved conclusive. Validation of the periodicity of growth band formation was attempted in the present study, but was not possible as no long-term recaptures of animals at liberty were made. Although the method of CEA verification statistically supported an annual cycle, like previous studies the results were ambiguous.

The difficulty of achieving validation in wide ranging sharks is an issue that has been particularly poignant for *S. lewini*. Its implications for both conservation and management are evident in demographic modelling of *S. lewini* populations, where greatly differing estimates of population productivity are obtained depending on whether annual or biannual growth band pairs are assumed e.g. Cortés (2002), Liu and Chen (1999). In the present study two reasons were used to justify the assumption that band pairs were formed annually. Firstly annual band pairs have now been validated for two other species of hammerheads, including *S. mokarran* in the present study (Parsons, 1993; Passerotti *et al.*, 2010). Secondly, evidence for annual bands has been found in many other chondrichthyan growth studies (Campana *et al.*, 2002; Simpfendorfer *et al.*, 2002b; McAuley *et al.*, 2006; Pierce and Bennett, 2009).

Why the various indirect methods (e.g. marginal increment ratio, CEA) for verifying band pair timing in *S. lewini* have failed to produce a convincing pattern is unclear, but it is probably related to small sample sizes. Campana (2001) stressed the limitations of these methods, especially when multiple age groups are combined or sample sizes are insufficient. In the present study, the timing of band pair deposition for *S. mokarran* appeared to coincide with reproduction. It follows that if growth band formation in *S. lewini* also coincides with reproduction, then the reproductive strategy, which is only partially seasonal, may have obscured any patterns in the CEA.

If all growth studies of *S. lewini* are transformed to have annual growth band deposition, then global estimates of growth *S. lewini* are relatively similar (Figure 4.9 b), although it should be noted that the same argument can be made in reverse. In the present study, the oldest male aged was 21 years, while the maximum age of females could not be established due to a lack of adults. In the northwest Atlantic, Piercy *et al.* (2007) aged both sexes up to 30.5 years of age. If the data of Chen *et al.* (1990) are transformed to annual bands, maximum ages are 28 and 22 years for females and males, respectively. At present, empirical evidence is lacking to support such longevity in *S. lewini* as none of the above estimates are validated. For example, the maximum

time at liberty in any tagging study is ~10 years (Kohler *et al.*, 1998). It is worth noting however that extensive study of young of the year individuals in Hawaii indicates that growth rates during the first year are relatively slow (96 mm.y^{-1}) and are characterised by periods of weight loss immediately after birth (Lowe, 2002; Duncan and Holland, 2006). This is compared with a mean first year growth of 630 mm in females and 540 mm in male *S. lewini* predicted by the original, untransformed models of Chen *et al.* (1990). Such rapid growth has so far only been observed in captive situations (Clarke, 1971). Based on the available evidence, it is hypothesised that *S. lewini* is long-lived (at least 20-30 yrs) and is slow-growing throughout its range.

4.4.2 Life history of *Sphyrna mokarran*

The present study of *S. mokarran* provides a valuable contribution to our understanding of the life history of a widely distributed but poorly understood species that has been heavily impacted by fisheries throughout much of its range. On the east coast of Australia, *S. mokarran* was present in shallow tropical waters at a wide range of lengths $>795 \text{ mm } L_{ST}$. Despite extensive sampling of near-shore habitats, no neonates were captured. This supports the findings of other studies that suggest this species does not use discrete coastal nursery areas and that pupping probably occurs further offshore (Stevens and Lyle, 1989; Hueter and Tyminski, 2007). Few pregnant females were recorded, but from the limited data available, timing of birth would appear to occur around October to November on the east coast, slightly earlier than that reported by Stevens and Lyle (1989) for northern Australia. Sexual segregation in this species was less pronounced than in *S. lewini*, however juveniles of both sexes and adult females appear to be much more common in inshore tropical areas (Chapter 2), while adult males may be relatively more common in temperate waters (Macbeth *et al.*, 2009).

The growth rate of *S. mokarran* in the present study ($k = 0.079 \text{ yr}^{-1}$) was considerably slower than found by Piercy *et al.* (2010) for the northwest Atlantic and Gulf of Mexico ($k = 0.16 \text{ yr}^{-1}$, males; and $k = 0.11 \text{ yr}^{-1}$, females). The asymptotic length on the east coast of Queensland ($L_{\infty} = 4027 \text{ mm } L_{ST}$) was also larger than those calculated by Piercy *et al.* (2010) (3346 mm L_{ST} , males; and 3892 mm L_{ST} , females). This difference translated into much faster early growth in Atlantic *S. mokarran*, with growth rates approaching 400 mm.yr^{-1} in the first year of life compared with around 250 mm.yr^{-1} off eastern Australia. The slower first year growth of Australian *S. mokarran* was supported by the existence of age-0 individuals in the range of ~850-950 mm L_{ST} approximately one year after birth (Figure 4.5 b). As a direct consequence of this, age at 50%

maturity in Australia occurred at 8.3 years of age compared with an estimated 5 – 6 years in the Atlantic. The maximum ages of males (31.7) and females (39.1) in the present study were somewhat lower than those obtained by Piercy *et al.* (2010) (42 years, males; 44 years, females), however few large animals (especially males) were sampled.

Although this is the first study to statistically establish age-at-maturity of *S. mokarran*, several studies have previously examined length-at-maturity. Across northern Australia Stevens and Lyle (1989) reported that maturity occurred at 2250 mm L_{ST} for males and 2100 mm L_{ST} for females. Although L_{ST50} was not established in that study, length-at-maturity occurred over a similar length range to the current study and was also highly variable. It is concluded that length-at-maturity of *S. mokarran* does not appear to differ greatly throughout its range in Australian waters. However, elsewhere in its range, *S. mokarran* appears to mature at considerably greater lengths. Cliff (1995) found that females matured at 3370 mm L_{ST} and males at 3090 mm L_{ST} off the coast of South Africa, while Piercy *et al.* (2010) reported a median length-at-maturity of 2850 mm L_{ST} for females and 2380 mm L_{ST} for males in the northwest Atlantic and Gulf of Mexico.

4.5 CONCLUSIONS

The results of this study suggest that in the waters off eastern Australia *S. lewini* and *S. mokarran* are long-lived and slow-growing species, although some components of the population may grow faster than others (e.g. tropical *S. lewini* males). Although both species have high fecundities in comparison to many other shark species (Last and Stevens, 2009), assumptions that this will translate into greater population growth rates should be considered carefully given the lack of empirical measurements of first year survival rates for sharks in general and these species in particular (Bush and Holland, 2002; Heupel and Simpfendorfer, 2002; Duncan and Holland, 2006). Therefore, despite being assessed by the IUCN as Least Concern in Australian waters (Cavanagh *et al.*, 2003), these species should be managed cautiously, especially in light of the recently reported declines off eastern Australian (de Jong, 2009) and in many other parts of their range (Dudley and Simpfendorfer, 2006; Ferretti *et al.*, 2008; Hayes *et al.*, 2009). The recent closure of 33% of the Great Barrier Reef World Heritage Area to commercial fishing in 2004 (GBRMPA, 2009) is likely to be beneficial to populations of these species off eastern Australia, although a better understanding of their movements and distributions relative to protected areas is also necessary. For *S. lewini* specifically, it is not possible to accurately assess the potential threats to this species without first identifying the location of the adult female component of the

stock. Since females are likely to be more pelagic than males and potentially migratory (Clarke, 1971; Klimley, 1987; Stevens and Lyle, 1989), Australian stocks may be shared with nearby countries (e.g. Indonesia, Papua New Guinea) or extend well into the high seas. Future work should therefore prioritise the demarcation of adult female component of the stock.

Additional future work on *S. lewini* must also prioritise age validation of this species. This is a major issue with profound implications for fisheries management and conservation. Since all indirect age verification methods have so far proved inconclusive, direct age validation methods (e.g. mark, tag, recapture or bomb radiocarbon validation) appear to be the only way to conclusively resolve whether growth bands are formed annually or biannually in this species and therefore confirm its longevity.

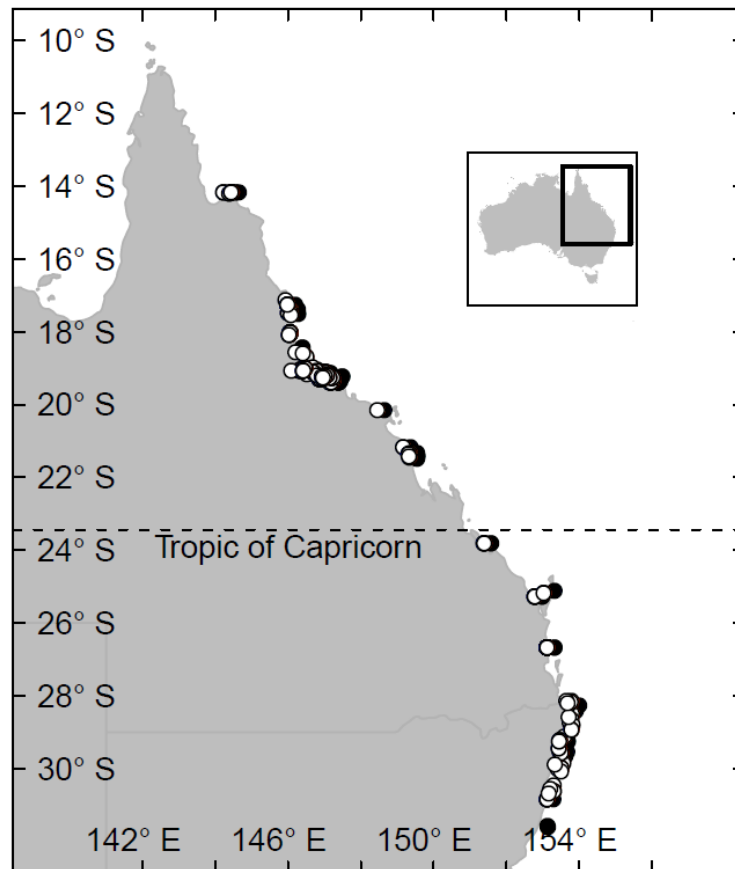


Figure 4.1 Location of the study area showing sampling locations of *Sphyrna lewini* (○) and *Sphyrna mokarran* (●) off eastern Australia. Apparent spatial differences in growth and maturity of male *S. lewini* were examined by including region as a factor in growth and maturity analyses. Region was a two level factor (tropic and temperate) with samples separated into the two nominal regions by the Tropic of Capricorn.

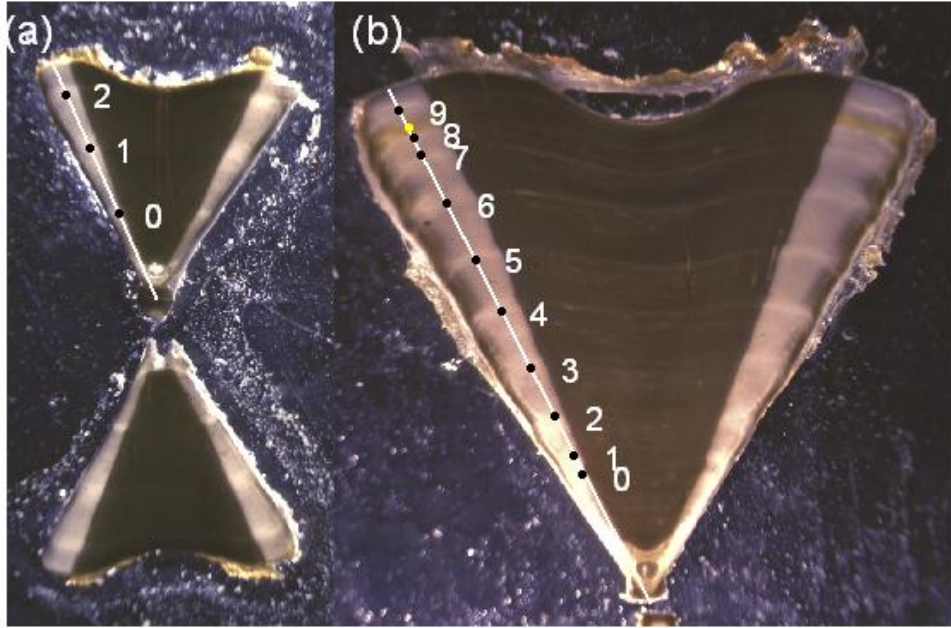


Figure 4.2 Sectioned vertebrae centrum from an 1145 mm L_{ST} male *Sphyrna lewini* with two growth band pairs visible (a), and a 2598 mm L_{ST} male *Sphyrna mokarran* with nine growth band pairs visible (b). The vertebrae centrum in (b) is from individual GHH4 (Table 4.1) that was injected with calcein and recaptured after 467 days at liberty. Translucent bands on the vertebrae are denoted by ● and the calcein mark denoted by ●. Age 0 corresponds to the birth mark.

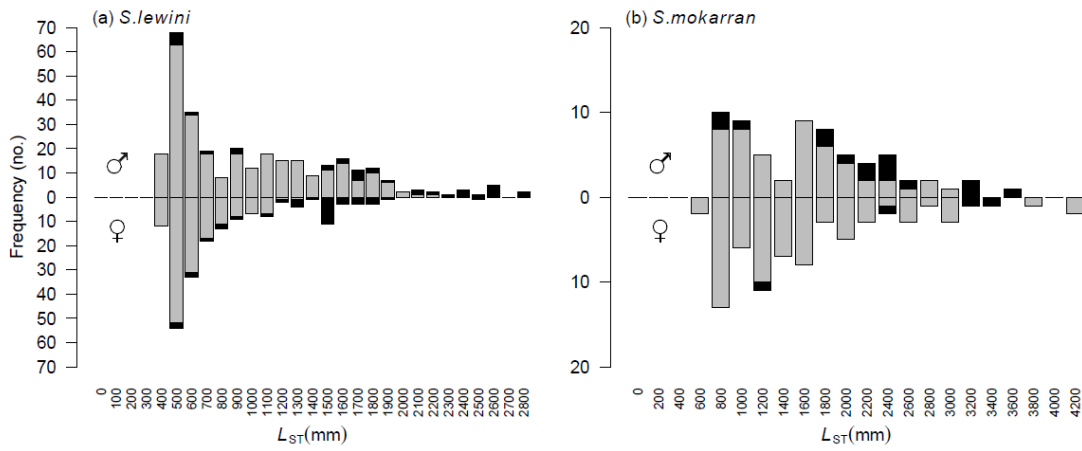


Figure 4.3 Length-frequency distributions of (a) *Sphyrna lewini* (n = 518) and (b) *Sphyrna mokarran* (n = 142) specimens collected off eastern Australia between December 2005 and May 2010. Bar colour denotes capture location: tropic ■ or temperate ■.

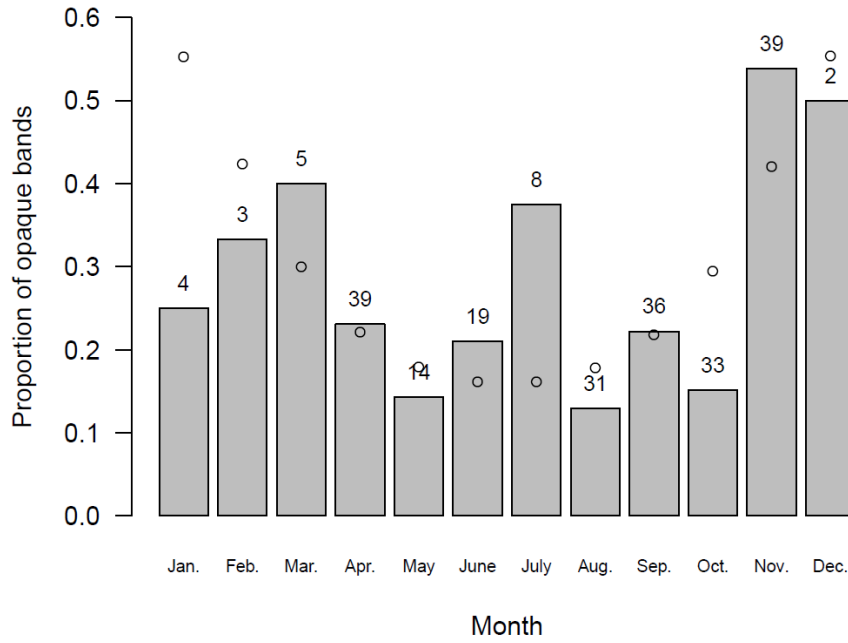


Figure 4.4 Monthly proportions of opaque bands present on the outer margin of vertebrae centra for *Sphyrna lewini*. Total sample sizes in each month are denoted by numbers above bars. Open circles indicate the best-fit model suggesting an annual cycle of band formation.

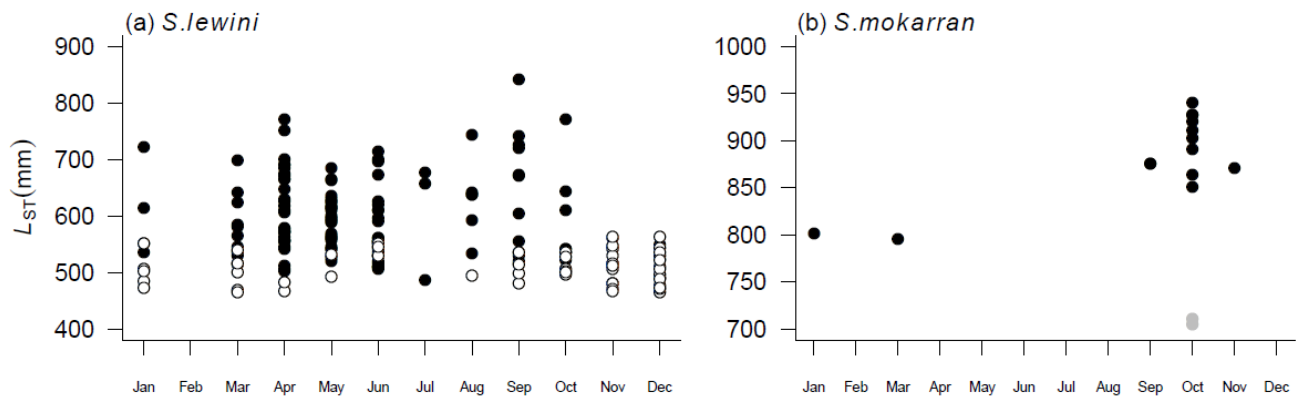


Figure 4.5 Occurrence and length of age 0 individuals (●), neonates (○), and near-term embryos (◐) throughout the year, used to determine the duration of the first growth increment.

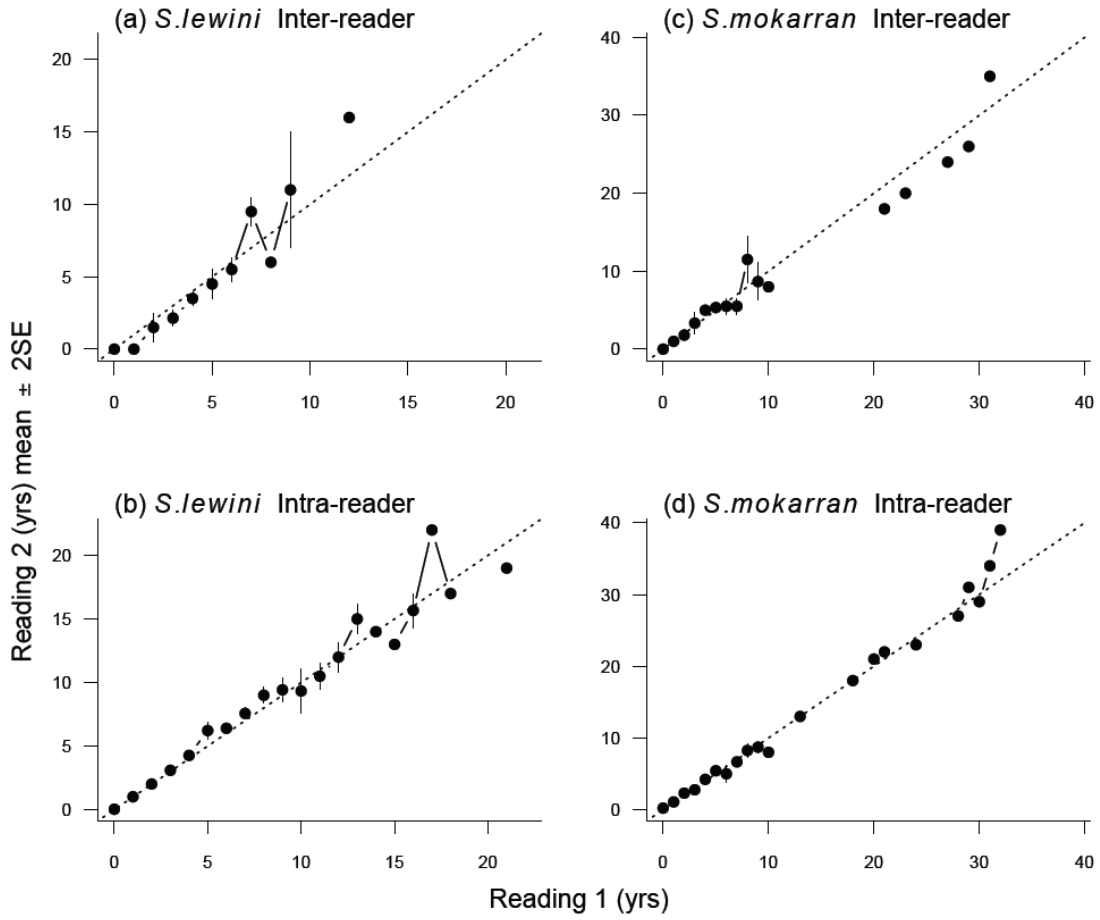


Figure 4.6 Inter- and intra-reader age-bias plots for *Sphyrna lewini* (a–b) and *Sphyrna mokarran* (c–d).

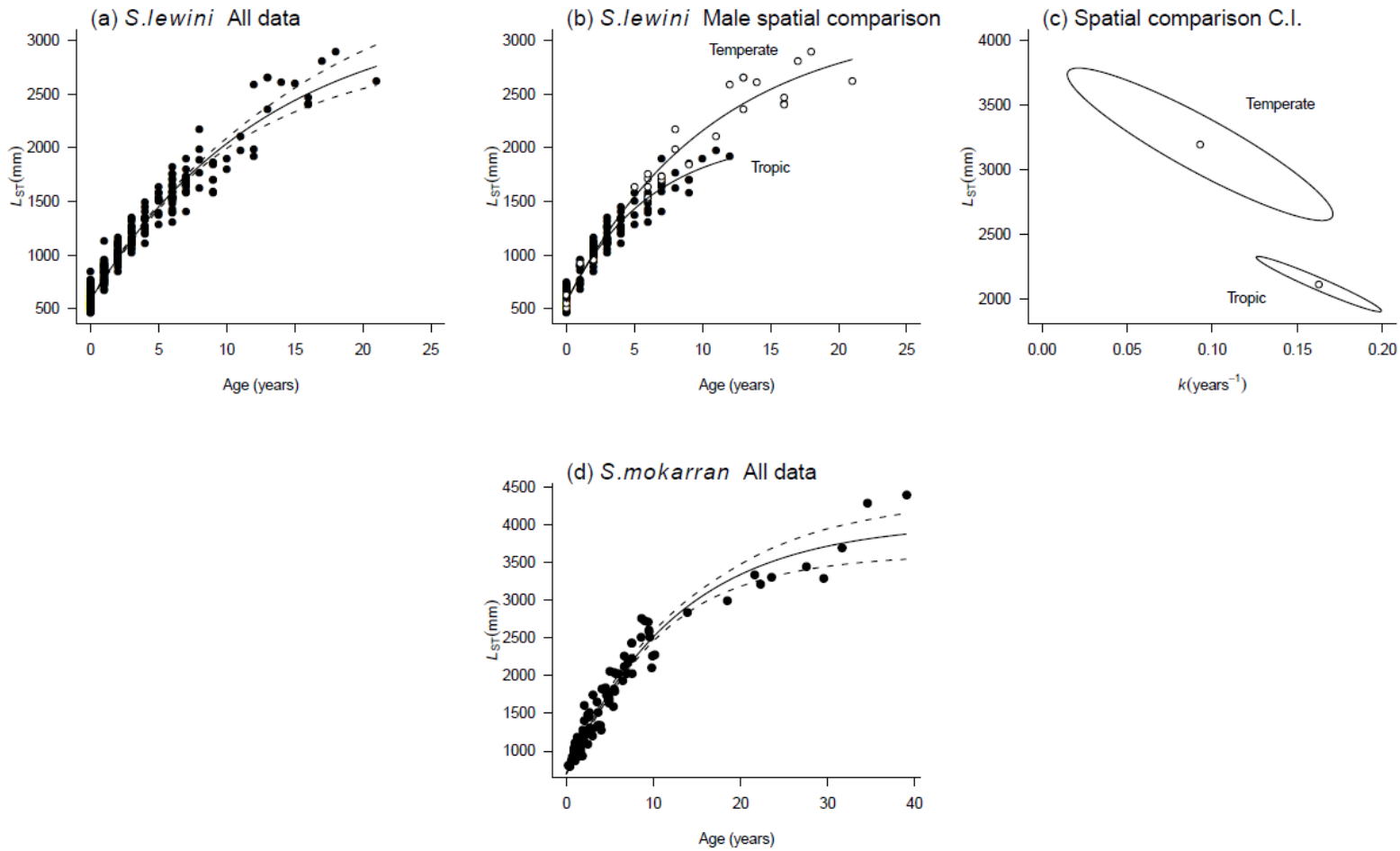


Figure 4.7 Length-at-age determined by vertebral analysis for *Sphyrna lewini* (a–b) and *Sphyrna mokarran* (d). Solid lines are fitted von Bertalanffy growth models and dashed lines in (a) and (d) are 95% confidence intervals. Approximate confidence intervals for the spatial comparison of male *S. lewini* growth in (b) are provided in (c) and highlight the difference in growth rate, k , and L_{∞} parameters.

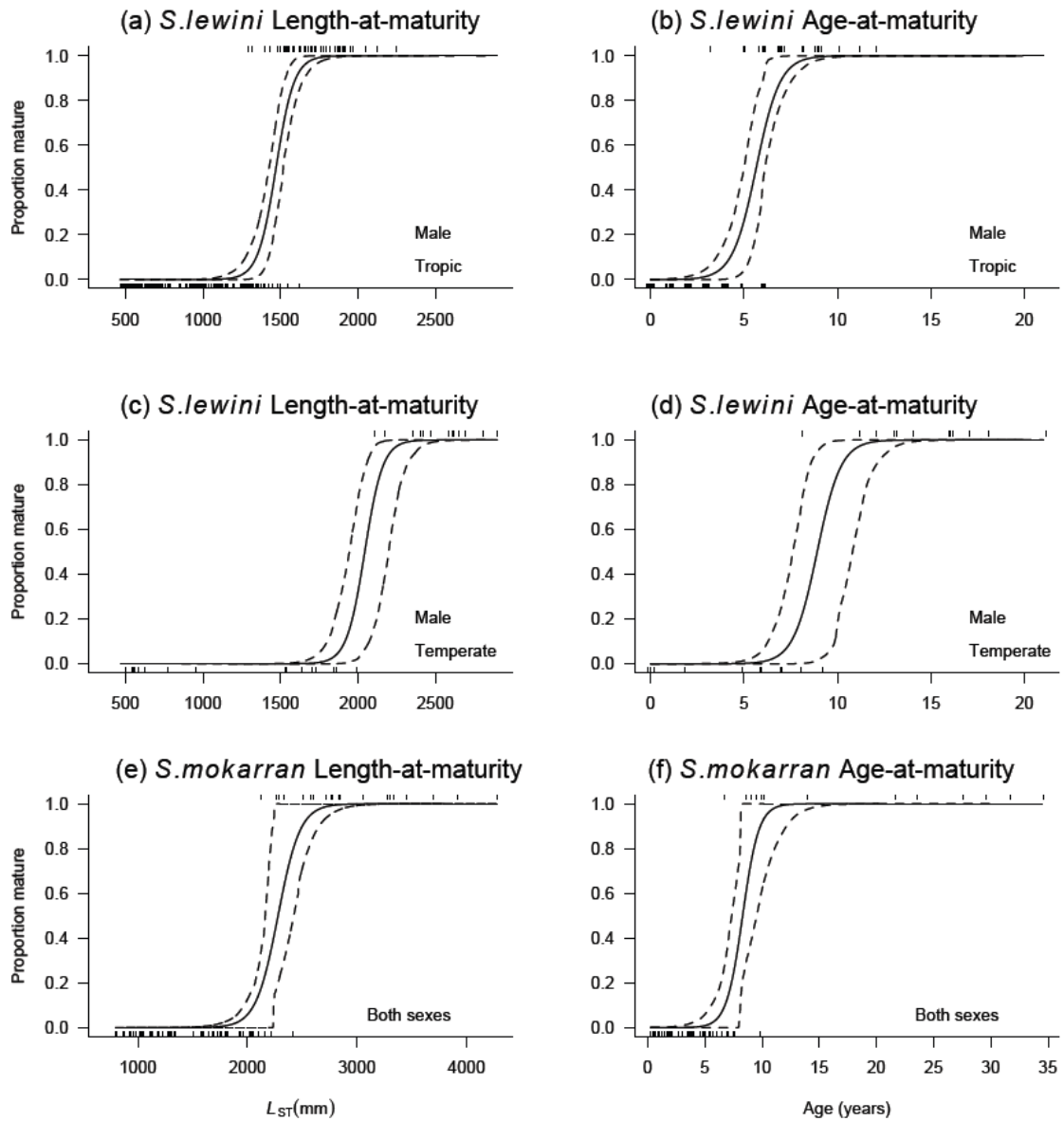


Figure 4.8 Length- and age-at-maturity ogives for *Sphyrna lewini* in tropical and temperate waters (a–d) and *Sphyrna mokarran* from all latitudes sampled (e–f) during this study. Solid lines are the expected proportion of population mature at a given length and dashed lines are 95% confidence intervals. Rug plots indicate observed data points.

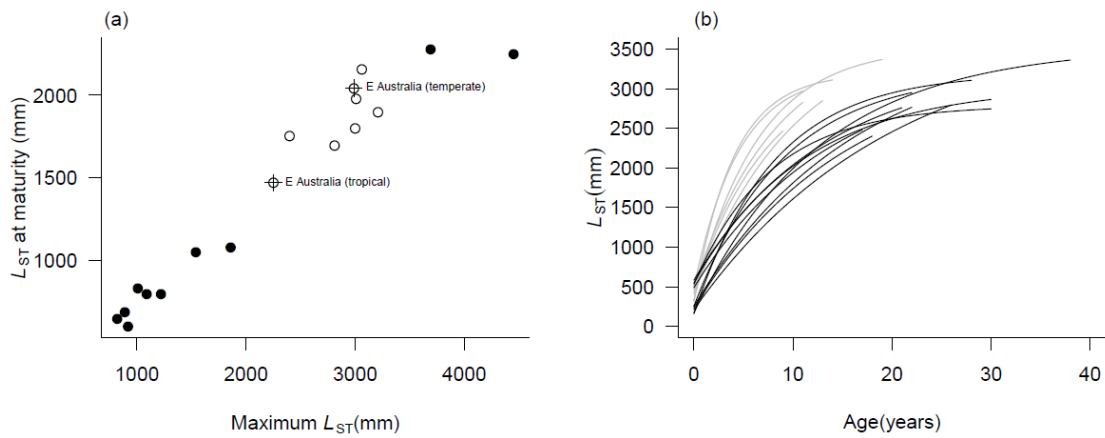


Figure 4.9 Synthesis of life history data from published studies on hammerheads indicating (a) how maximum length predicts length at maturity in male hammerhead sharks (where ○ denotes *S. lewini* and ● denotes all other hammerhead species), and (b) a comparison of all growth estimates for both sexes when growth bands pairs are assumed to be formed annually. Grey lines in (b) are original growth trajectories in studies that have assumed biannual growth band deposition.

Table 4.1 Recapture details of five calcein-marked *Sphyrna mokarran* at liberty for 126 – 467 days. Two individuals at liberty for 353 and 467 days formed a single band pair, supportive of an annual cycle for band pair deposition in this species.

	Date released	$L_{ST\ Rel\ ease}$ (mm)	Date recaptured	$L_{ST\ Recap}$ (mm)	Days at liberty	Growth (mm)	Band pairs formed
GHH1	18-November-2008	2037*	06-November-2009	2160	353	123	1
GHH2	26-November-2008	1760	28-April-2009	1820	153	60	
GHH3	26-November-2008	1820	01-April-2009	1892*	126	72	0
GHH4	16-January-2009	2340	28-April-2010	2598	467	258	1
GHH5	22-October-2009	1284	26-April-2010	1470	186	186	0

$L_{ST\ Rel\ ease}$, Stretch total length at release; $L_{ST\ Recap}$, Stretch total length at recapture,

* length unavailable, estimated via back or forward calculation

Table 4.2 Summary of five *a priori* growth models fitted to length-at-age data for two species of hammerhead shark. Models are ranked in terms of performance (best to worst with the best in bold) based on computed values of small-sample, bias-adjusted Akaike's Information Criteria (AIC_c). Akaike differences (Δ) and Akaike weights (w) show the relative support for other models. The number of parameters in each model (+1 for variance) is given by K.

Species	Model	K	AIC_c	Δ	w	R.S.E.
<i>Sphyrna lewini</i>	VBF3	4	3647.29	0.00	1.0000	104.13
	Schnute	5	3709.97	62.68	0.0000	120.85
	Gompertz	4	3710.37	63.08	0.0000	113.08
	VBF2	3	3762.96	115.67	0.0000	151.96
	Logistic	4	3943.59	296.30	0.0000	112.65
<i>Sphyrna mokarran</i>	VBF2	3	1043.10	0.00	0.7262	180.25
	VBF3	4	1045.06	1.95	0.2738	180.98
	Gompertz	4	1068.84	25.73	0.0000	203.83
	Schnute	5	1095.69	52.58	0.0000	231.75
	Logistic	4	1097.79	54.69	0.0000	235.59

Table 4.3 Best fit parameter estimates (with 95% CI) in preferred growth models for two species of hammerhead shark. Parameters are asymptotic length (L_{∞}), length at birth (L_0) and growth completion rate (k). The sample size of each analysis is given by N.

Species	Sex	Region	Model	N	L_{∞} (mm)	L_0 (mm)	k (yr ⁻¹)
<i>Sphyrna lewini</i>	Both	Pooled	VB3	392	3305 (2924, 3934)	582 (572, 593)	0.077 (0.059, 0.094)
	Male	Tropic	VB3	200	2119 (1943, 2304)	565 (553, 579) ¹	0.163 (0.136, 0.196)
	Male	Temperate	VB3	30	3199 (2616, 4042)		0.093 (0.026, 0.166)
<i>Sphyrna mokarran</i>	Both	Pooled	VB2	100	4027 (3638, 4545)	700 ²	0.079 (0.064, 0.095)

¹ L_0 was not significantly different in the regional comparison for males ² L_0 was fixed at 700 mm in the best fit model for *S. mokarran*

Table 4.4 Hypothesis testing for the effect of region on von Bertalanffy growth parameters for male *Sphyrna lewini*. Four hypotheses (H1–H4) were tested against the null hypothesis (H0) using likelihood ratio tests, where LL is the computed negative log-likelihood for a model, χ^2 is test statistic, d.f. is the degrees of freedom and P is the probability of significance.

Potential process	LL	χ^2	d.f.	P
H0 All parameters differ between region	1369.7	-	7	-
H1 L_∞ is the same between regions	1386.2	32.896	6	<0.001
H2 k is the same between regions	1377.5	15.566	6	<0.001
H3 L_0 is the same between regions	1369.8	0.037	6	0.848
H4 All parameters are the same between regions	1407.7	75.985	4	<0.001

Table 4.5 Summary of logistic regression analysis of length- and age-at-maturity stage for two species of hammerhead shark. The effects of the factors sex and region (tropical and temperate) on maturity stage were also examined, and the best model was chosen as the one that minimised the small-sample, bias-adjusted form of Akaike's Information Criteria (AIC_C). Akaike differences (Δ), Akaike weights (w), residual deviance and residual degrees of freedom show the relative performance of competing models. K is the number of estimated regression parameters. The models with the most support are in bold.

Species	Model	K	AICc	Δ	w	Residual deviance
<i>Sphyrna lewini</i>	Stage~L_{ST}+Region	3	52.72	0.00	0.5449	46.63
	Stage~L _{ST} +Region+L _{ST} :Region	4	53.08	0.36	0.4551	44.93
	Stage~L _{ST}	2	95.84	43.12	0.0000	91.80
	Stage~Age+Region	3	45.13	0.00	0.7348	39.00
	Stage~Age+Region+Age:Region	4	47.18	2.04	0.2650	38.96
	Stage~Age	2	61.22	16.08	0.0002	57.15
<i>Sphyrna mokarran</i>	Stage~L_{ST}	2	23.16	0.00	0.6231	19.01
	Stage~L _{ST} +Sex	3	25.11	1.95	0.2350	18.82
	Stage~L _{ST} +Sex+L _{ST} :Sex	4	26.12	2.96	0.1418	17.62
	Stage~Age	2	20.54	0.00	0.5948	16.35
	Stage~Age+Sex	3	21.89	1.34	0.3044	15.50
	Stage~Age+Sex+Age:Sex	4	24.10	3.55	0.1008	15.44

Table 4.6 Summary of preferred logistic regression models used to determine length- and age-at-maturity of two species of hammerhead shark. Parameter values (with 95% CI) are given for the logistic regression model $P(x) = 1/(1 + \exp(a + bx))$, where $P(x)$ is the proportion of individuals mature at a given length or age x , and a and b are fitted regression coefficients. L_{ST50} and A_{50} (with 95% CI) are populations estimates of stretch total length (mm) and age (years) at 50% maturity, n is the number of mature animals, and N is the total number of animals.

Species	Model	Sex	Region	a	b	L_{ST50} / A_{50}	n	N
<i>Sphyrna lewini</i>	Stage~ L_{ST} +Region	Male	Tropic	-25.29 (-38.72, -17.44)	0.017 (0.026, 0.119)	1471 (1423, 1519)	56	233
			Temperate	-35.12 (-53.83, -23.49)		2043 (1934, 2182)	14	31
	Stage~Age+Region	Male	Tropic	-8.90 (-13.94, -5.75)	1.575 (1.028, 2.368)	5.7 (5.1, 6.2)	25	160
			Temperate	-14.03 (-23.36, -7.75)		8.9 (7.5, 10.8)	13	27
<i>Sphyrna mokarran</i>	Stage~ L_{ST}	Both		-22.63 (-39.34, -13.74)	0.010 (0.006, 0.0185)	2279 (2149, 2429)	22	85
	Stage~Age	Both		-11.76 (-24.07, -5.65)		1.418 (0.630, 2.818)	8.3 (7.4, 9.5)	15

Chapter 5. Vertebral counts highlight a disparity in current genetic methods used to distinguish between the morphologically similar Australian blacktip shark and common blacktip shark



Plate 5. Dissection of a blacktip shark to help determine species (September 2010).

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5.0 RESEARCH NOTE

Taxonomy, the science of describing and delimiting species, plays a critical role in both biological conservation and fisheries management (Mace, 2004). It therefore seems particularly relevant for the Chondrichthyes, a class of animals that are sensitive to anthropogenic impacts and as such require careful conservation planning and fisheries management to prevent population declines (Walker, 1998; Stevens *et al.*, 2000a). Recent taxonomic separation of several chondrichthyan species supports this notion. For example, the resurrection of *Squalus suckleyi* (Girard 1855) as distinct from the widely distributed *S. acanthias* Linnaeus 1758 will allow better fisheries management of these commercially exploited species which differ in growth rates by an order of magnitude (Ebert *et al.*, 2010). The recent re-description of the genus *Manta* into two separate species will similarly allow a more focused approach to conservation of manta rays (Marshall *et al.*, 2009).

Molecular methods play an important role in species delimitation, especially for cryptic species that have few or no known external diagnostic morphological features. Two such cryptic species are the Australian blacktip shark, *Carcharhinus tilstoni* (Whitley, 1950), and the common blacktip shark, *Carcharhinus limbatus* (Müller & Henle 1839). These species occur sympatrically in the waters off northern Australia (Last and Stevens, 2009) where they make an important contribution to a number of commercial fisheries (Stevens and Wiley, 1986; Macbeth *et al.*, 2009; Bensley *et al.*, 2010) (Chapter 2). The high natural abundance and biomass of *C. tilstoni* (Stevens and Davenport, 1991), which is endemic to northern Australia, makes this species a dominant top predator in northern Australia's coastal ecosystems. In addition to supporting a number of commercial fisheries, *C. tilstoni* likely has an important role in regulating ecosystem function. *Carcharhinus limbatus* has, until recently, been perceived to be relatively rare in northern Australian waters (Ovenden *et al.*, 2010). This widespread species is exploited by fisheries throughout its range (Compagno *et al.*, 2005). Hampering sustainable management of blacktip sharks in northern Australia is their similarity in appearance. As no known external morphological differences exist, these species are thought to be reliably distinguished at all sizes only by counts of their vertebrae (Stevens and Wiley, 1986) or using molecular techniques (Lavery and Shaklee, 1991; Ovenden *et al.*, 2006).

The apparently identical external appearance of *C. tilstoni* and *C. limbatus* belies large differences in the biology and life history between these species. Indeed, phylogenetic work suggests that *C. limbatus* is more closely related to the graceful shark, *Carcharhinus amblyrhynchoides* (Whitley 1934) than *C. tilstoni* (Lavery, 1992; Ward *et al.*, 2008; Ovenden *et al.*, 2010). Yet demonstrating the differences in biology between *C. tilstoni* and *C. limbatus* has been difficult due to a lack of directed studies of *C. limbatus* in Australian waters. Stevens and Wiley (1986) found that length at maturity of male *C. limbatus* occurred at approximately 1800 mm stretched total length, L_{ST} , in the Arafura Sea, approximately 700 mm larger than the length at maturity of *C. tilstoni* from the same region. Observations of *C. limbatus* in excess of 2600 mm L_{ST} from northern New South Wales waters confirm the vast size difference compared to *C. tilstoni*, which appears to rarely exceed 1600-1800 mm L_{ST} (Stevens, 1984; Stevens and Wiley, 1986; Macbeth *et al.*, 2009).

Two recent molecular studies on blacktips in Australia have reported dramatic changes to the abundance and distribution of *C. tilstoni* and *C. limbatus* in the waters surrounding Australia. Ovenden *et al.* (2010) found the ratio of *C. tilstoni* to *C. limbatus* was approximately equal, in stark contrast to the ratio of 300:1 previously reported by Stevens and Wiley (1986). Boomer *et al.* (2010) also reported a southerly increase in the range of *C. tilstoni* in excess of 1000 km on the east coast of Australia. Such dramatic and rapid shifts in the abundance and distribution of *C. tilstoni*, Australia's most abundant large, tropical shark, raise questions about the drivers of this change, its potential cascading effects on the ecosystem, and implications for fisheries management.

However, the basis for such claims may be unfounded, as there has been little or no validation of the current methods used for distinguishing between the two species. Initial genetic separation of *C. tilstoni* and *C. limbatus* was based on individuals distinguished only by pelvic fin colouration (Lavery and Shaklee, 1991), a method no longer considered reliable (Last and Stevens, 2009). Vertebral count ranges used to distinguish the species are similarly based on a relatively small number of samples: 23 *C. tilstoni* and 14 *C. limbatus* (Stevens and Wiley, 1986). Ovenden *et al.* (2010) confirmed the identity of their specimens using both genetic methods and vertebral counts, however used only eight individuals. Finally, Boomer *et al.* (2010) provide no vertebral counts or other information on their samples, despite advocating a multifaceted approach to species identification. Clearly there is an urgent need to validate the current genetic method and vertebral count methods used to distinguish between these species.

In the present study, *C. tilstoni* and *C. limbatus* samples were collected during vessel-based observer study of sharks from a commercial gillnet fishery operating within the Great Barrier Reef World Heritage Area (Chapter 2). Additional samples were purchased from fishers or obtained opportunistically using fishery-independent sampling methods. All samples were collected from shallow waters (<25 m depth) between January 2006 and December 2010 between Princess Charlotte Bay (14°15'S) and Moreton Bay (27°12'S) on the east coast of Queensland, Australia. The stretched total length, L_{ST} , of each individual was measured in millimetres. Given the limited access to catch by fishery observers, genetic methods were employed as the principal method of identifying blacktip sharks. Muscle tissue samples were collected from each individual and stored frozen, prior to being stored in a solution of 70–100% ethanol. Genetic identification of individuals based on mitochondrial DNA was carried out by the Department of Employment, Economic Development, and Innovation at the Molecular Fisheries Laboratory in Brisbane, Queensland. The protocols for genetic identification are described by Ovenden *et al.* (2006) and Ovenden *et al.* (2010).

In addition to identification using genetic methods, vertebral counts of a sub-sample of individuals were collected opportunistically as a supplementary form of identification. Pre-caudal vertebrae (PCV) counts were made of all vertebrae anterior to the pre-caudal pit. This was done by severing and removing the caudal fin at the anterior edge of the pre-caudal pit and then by running a knife from tail to the head to remove flesh from one side of the animal. This method exposed all vertebrae clearly, including those at the base of the skull. Vertebrae were then counted sequentially from the tail to head in groups of 10 to minimise counting errors. Individuals with a PCV count <92 were considered as *C. tilstoni* and those with a PCV count >93 considered *C. limbatus* (Stevens and Wiley, 1986). As the majority of individuals were sampled during a fishery observer study and processed at-sea, vertebral counts were not always possible. To increase the total number of vertebral identifications, vertebral counts of one or more developing embryos from pregnant females were used to infer the identity of the mother.

Three life history characteristics were chosen to validate the accuracy of genetic and vertebral identification methods: length-at-birth, male clasper length and maturity stage, and female maturity stage. These characteristics were chosen because they were observed to differ noticeably between species and were measured during the course of regular sampling. Length-at-birth was inferred from neonate *C. tilstoni* and *C. limbatus* that were prolific in nearshore habitats during

spring and early summer. Both species utilise a reproductive mode of placental viviparity, so neonates were identifiable by the presence of an unhealed umbilical scar. Male outer clasper length (Compagno *et al.*, 2005) was measured as the distance from the tip of the clasper to the pelvic fin. Reproductive staging of animals was determined based on the descriptions of Walker (2005a) for clasper condition and uterus condition.

Lengths were obtained from a total of 961 individuals consisting of 475 males (555–1620 mm L_{ST}), 502 females (570–1930 mm L_{ST}) and 19 individuals of unknown sex (620–1030 mm L_{ST}). Using molecular methods, a genetic identity was obtained for a total of 641 individuals, consisting of 445 *C. tilstoni* (593–1930 mm L_{ST}) and 196 *C. limbatus* (620–1620 mm L_{ST}). Pre-caudal vertebrae counts were obtained directly from 202 individuals (568–1740 mm L_{ST}), and inferred indirectly from a further eight pregnant females (1553–1800 mm L_{ST}) by counting the vertebrae of 25 embryos (Figure 5.1). While most PCV values were either > 93 (*C. limbatus*) or < 92 (*C. tilstoni*) three individuals had a PCV of 93 and could not be assigned an identity based on their vertebral count. As such, a total of 207 individuals were assigned a vertebral identity. PCV counts were in the range of 83–110 and displayed two modal peaks (Figure 5.2). The mean (\pm s.d.) PCV of 108 *C. tilstoni* (PCV count < 92) was 86.12 ± 1.32 with values in the range of 83–89. The mean PCV of 124 *C. limbatus* (PCV count > 93) was 99.28 ± 2.36 with values in the range of 94–110. In total 189 individuals were identified using both genetic methods and vertebral counts (Table 5.1). Overall agreement between vertebral and genetic methods was 85.2%.

Disagreements appeared to be systematic rather than random and primarily occurred in individuals that were identified as *C. limbatus* using vertebral counts, but which were identified as *C. tilstoni* using genetics (Table 5.1).

Of the 207 individuals identified using vertebral counts, 120 were neonates, while of the 641 individuals identified using genetic methods, 104 were neonates. Using vertebral identification methods there was clear separation between the length-at-birth distributions of the two species (Figure 5.3); mean length at birth of *C. tilstoni* was 620 mm L_{ST} while mean length-at-birth of *C. limbatus* was 722 mm L_{ST} . Using genetic identification methods, the length-at-birth of *C. tilstoni* was bi-modal and overlapped considerably with *C. limbatus*, however mean length-at-birth of genetically identified *C. limbatus* was 722 mm L_{ST} , identical to the value obtained using vertebral counts.

Chapter 5. Vertebral counts highlight a disparity in current genetic methods used to distinguish between the morphologically similar Australian blacktip shark and common blacktip shark

Plotting male clasper length against L_{ST} showed a clear separation of clasper lengths into two cohorts at approximately 1000 mm L_{ST} (Figure 5.4 a). At this point, clasper length of some individuals (assumed to be *C. tilstoni*) elongated rapidly as they reached maturity, while others (assumed to be *C. limbatus*) remained undeveloped until at least 1620 mm L_{ST} (the largest individual measured). Few vertebral counts were made of large males, however from the limited data available, vertebral identifications appeared to match expected clasper lengths (Figure 5.4 b). Genetic identifications also generally matched expected clasper lengths, although at least one individual identified as *C. tilstoni* appeared to have life history characteristics of a *C. limbatus* (Figure 5.4 c).

Like male clasper length, female maturity stage data also separated into two biologically distinct cohorts (Figure 5.4 d); some animals attained maturity at approximately 1200 mm L_{ST} (assumed to be *C. tilstoni*) while others remained immature up to at least 1930 mm L_{ST} (assumed to be *C. limbatus*). Vertebral identification methods matched the expected maturity stage, with all immature individuals > 1200 mm L_{ST} identified as *C. limbatus* (Figure 5.4 e). This clear separation into two cohorts was not observed in the genetically identified individuals; two genetically identified *C. limbatus* had reproductive characteristics of *C. tilstoni*, while two genetically identified *C. tilstoni* had reproductive characteristics of *C. limbatus* (Figure 5.4 f).

These results confirm the existence of two reproductively isolated and sympatric species of blacktip sharks in the waters surrounding Australia, as previously recognised by a number of authors (Whitley, 1950; Stevens and Wiley, 1986; Lavery and Shaklee, 1991). Yet, there was only 85% agreement between the two established methods for distinguishing between them. Identification by vertebral counts was concordant with differences in life history between the two species and this was most compelling for the length-at-birth comparison. Using vertebral identification methods, length at birth was found to be normally distributed for both species (Figure 5.3 b) as would be expected based on the central limit theorem, and as has been observed for other sharks (Simpfendorfer, 2000). Conversely based on genetic identifications, while length-at-birth of *C. limbatus* was normally distributed, *C. tilstoni* was bi-modally distributed.

Comparison of clasper length and reproductive stage also showed the genetic identification method occasionally identified individuals as species that did not agree with their expected life history (e.g. small, mature individuals as *C. limbatus*, or large, immature individuals as *C. tilstoni*). Interspecific variation in life history traits is well documented in *C. limbatus* throughout

its range (Dudley and Cliff, 1993; Carlson *et al.*, 2006) and is a potential explanation for this observation. If this were caused by climatic differences, a gradient in life history parameters would be expected (Yamaguchi *et al.*, 2000). Yet the observed pattern in clasper development (Figure 5.4 a), which has previously been described by Stevens and Wiley (1986) is concordant with two discrete, reproductively isolated stocks or, more likely, species.

Disagreements between vertebral and genetic identification methods were systematic and occurred mainly in individuals that were identified as *C. limbatus* using vertebral methods and *C. tilstoni* using genetic methods. Combined with findings above, this suggests that based on genetic identification methods, approximately 15% of individuals had life history characteristics corresponding to the opposite species, and most of the time this occurred for *C. limbatus*. The present study suggested identification using vertebral counts was preferable to genetics, although it should be noted that the range of values for vertebral counts exceeded that previously known. Most values were within the range reported by Stevens and Wiley (1986) but a small number of individuals fell outside the range; three individuals had 83 and 93 PCV, and single values of 105, 107, 109 and 110 were also recorded. Measurement error, including miss-counting of vertebrae or miss-identification of species, cannot be discounted as the cause of this. It also seems likely that the range of PCV values that *C. tilstoni* and *C. limbatus* can have is actually broader than reported by Stevens and Wiley (1986). We suggest that PCV values for *C. tilstoni* are in the range of 83-91 or greater, and PCV values of *C. limbatus* are within the range of 94-110 or greater.

The present study has important implication for the management of blacktip shark populations in Australian waters as it appears that molecular identification methods cannot at present be used to distinguish conclusively between *C. tilstoni* and *C. limbatus*. Because the accuracy of genetic identification methods is still high (~85%), the findings of this study corroborate those of Ovenden *et al.* (2010) who reported a large increase in the relative abundance of *C. limbatus* in northern Australian waters. Based on the subsample of individuals identified using genetic methods (n = 445 *C. tilstoni* and n = 196 *C. limbatus*), this suggests a ratio of 2.27:1. Based on the subsample of individuals identified using vertebral methods (n = 108 *C. tilstoni* and n = 124 *C. limbatus*), a ratio of 0.87:1 is obtained. As sampling of individuals was not random, these ratios should not be considered a true estimate of relative abundance, yet they provide an indication that the relative abundance of *C. limbatus* on the east coast of Queensland is much greater than the previously reported (Stevens and Wiley, 1986).

Rapid changes in abundance of elasmobranch populations have frequently been reported in the literature, often in response to commercial fishing (Graham *et al.*, 2001). High and likely unsustainable levels of fishing for sharks, mackerel and tuna by a Taiwanese net fishery in the waters off northern Australia during the 1970s and 1980s may have been a driver for the large shift in abundance observed (Walter, 1981; Stevens and Davenport, 1991). Recent increases in numbers of *C. limbatus* could therefore be due to immigration and succession of these animals from less-fished southerly waters. Alternatively, the larger size (and presumably slower growth rates) of *C. limbatus* may have resulted in it being more rapidly impacted by Taiwanese fishing activities, hence its lower abundance at the time of previous study.

As no sampling was done south of Moreton Bay, Queensland, is not possible to confirm the findings of Boomer *et al.* (2010) that *C. tilstoni* has a much more southerly range in Australian waters than previously thought, although it seems possible that some of the individuals identified as *C. tilstoni* in that study may in fact have been *C. limbatus*. In the present study vertebral-identified *C. tilstoni* were recorded as far south as Moreton Bay supporting their assertion that *C. tilstoni* is indeed more southerly ranging on the east coast of Australia than previously thought. As *C. tilstoni* and *C. limbatus* can easily be distinguished based on their differing maturity stages at lengths > 1000 mm, length and reproductive data from animals in that study could potentially resolve this issue. Further to this point, given that life history characteristics can be used to distinguish between these species relatively easily at most sizes, the notion that these species can only be identified using vertebral or genetics methods should also be disregarded.

At a broader level, the unexpected findings of the present study emphasize the importance of an integrated approach to species identification rather than reliance on a single method (Schlick-Steiner *et al.*, 2010). This seems timely given the renaissance underway in chondrichthyan taxonomy (Ebert and Compagno, 2007; White and Kyne, 2010). Explaining the phenomenon described here is beyond the scope of this communication although the finding has since led to the discovery of hybridisation between *C. tilstoni* and *C. limbatus* (Morgan *et al.*, In review). This is the first reported instance of hybridisation in chondrichthyans and appears to be the cause of the disparity between genetic and vertebral identification methods. The existence of hybridisation between two of the three closely related, but biologically distinct, blacktip species that occur in Australian waters may indicate a need for re-evaluation of taxonomy within this group.

This study also confirms the need for re-evaluation of management measures in tropical, Australian shark fisheries, which presently assume that the relatively rapid-growing *C. tilstoni* dominates the catch. Overall, this finding perhaps best re-iterates how limited our understanding of chondrichthyan biology is, when such a simple disparity in identification of two abundant, coastal sharks can be overlooked despite at least 40 years of commercial harvest.

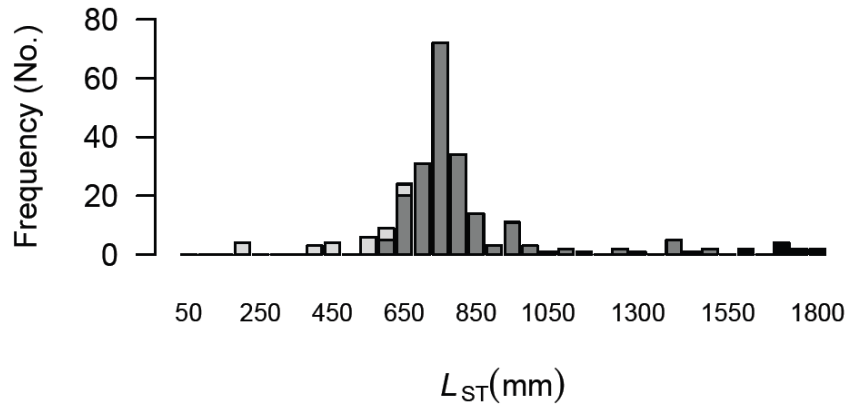


Figure 5.1 Length frequency of individuals that were identified by counting the number of pre-caudal vertebrae. Vertebral counts were obtained directly from most individuals ■ although the identity of eight pregnant females ■ was also inferred from counting the vertebrae of 25 developing embryos ■.

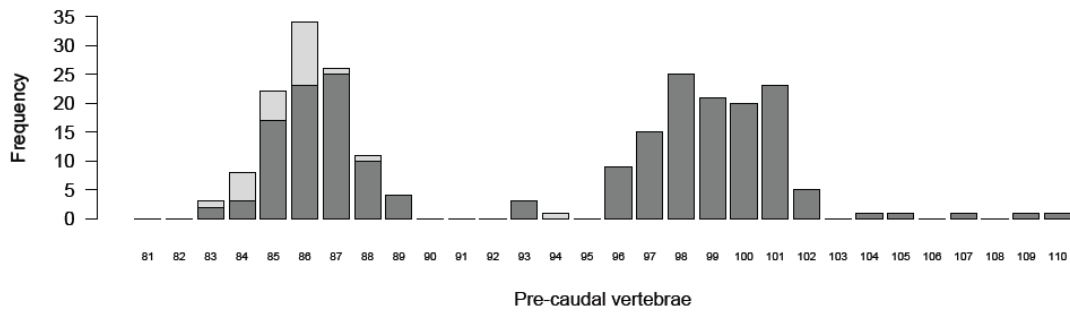


Figure 5.2 Number of pre-caudal vertebrae in 191 post-natal (■) and 21 pre-natal individuals (□).

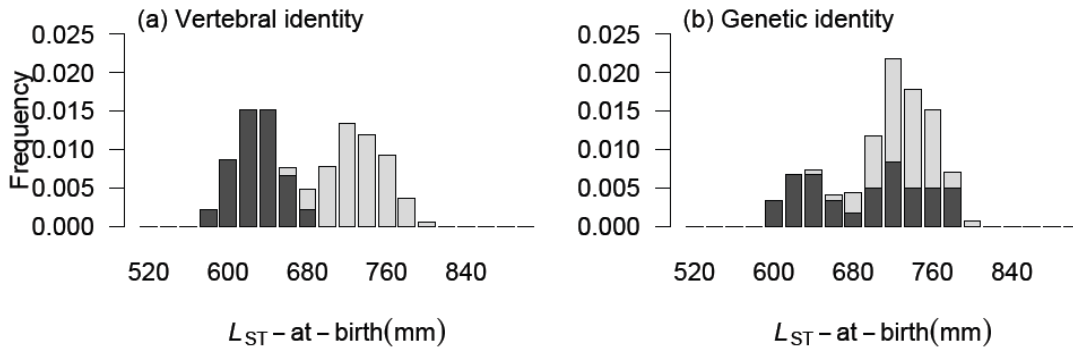


Figure 5.3 A comparison of length-at-birth frequency distributions obtained using the two identification methods. Individuals identified as *Carcharhinus tilstoni* are denoted by ■ and those identified as *C. limbatus* are denoted by □. Based on vertebral identification methods (a), length-at-birth distributions showed a clear separation, however this was not seen when using genetic methods (b).

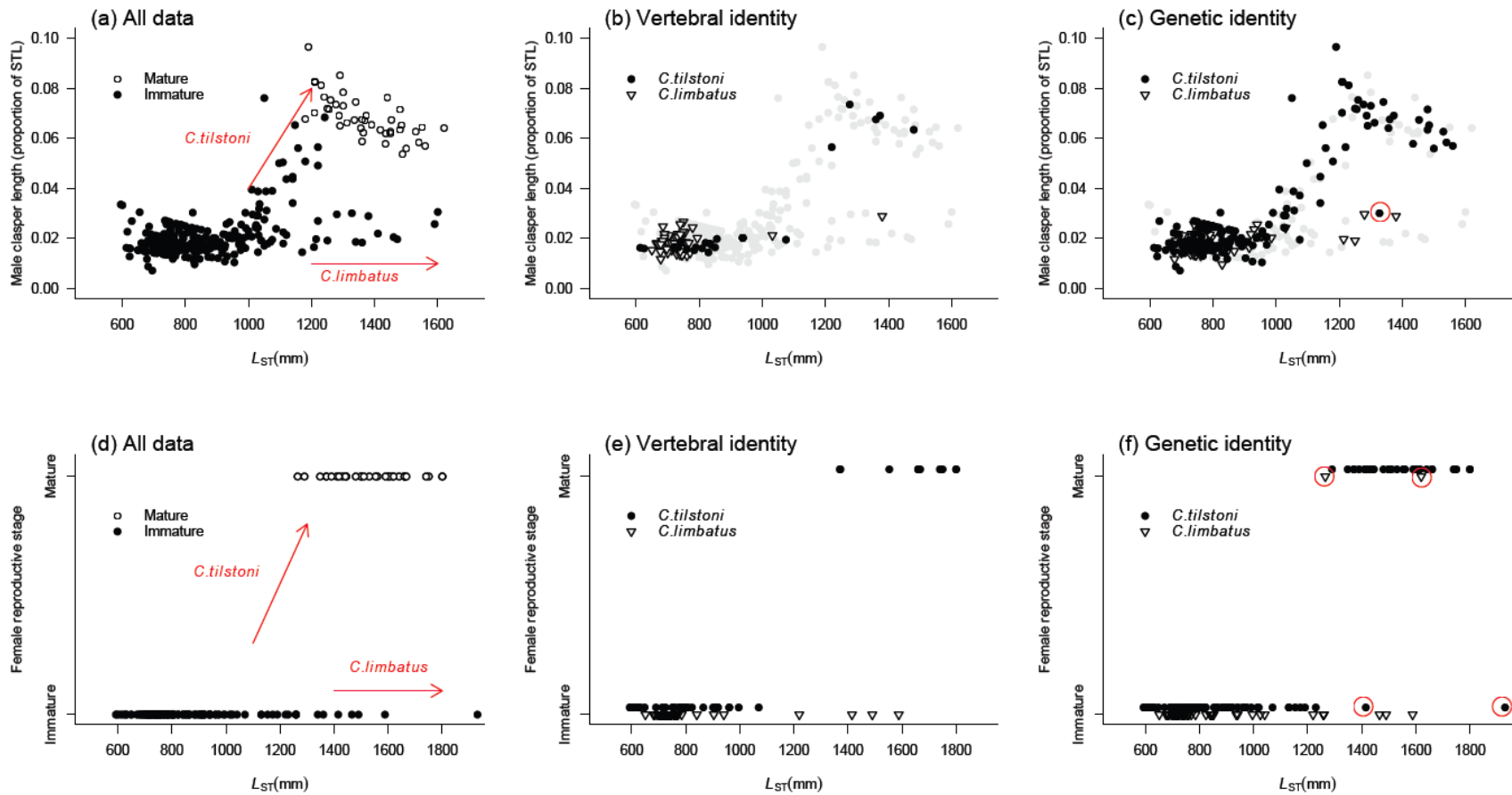


Figure 5.4 The contrasting length at-maturity of *Carcharhinus tilstoni* and *C. limbatus* based on male clasper length (a–c) and female uterus stage (d–f). The red arrows highlight the separation of the two species into distinct groups that occurs because *C. tilstoni* matures at a much smaller length than *C. limbatus*. While vertebral identification methods were consistent with these groupings, genetic methods showed some inconsistencies (red circles).

Table 5.1 Tabulation of agreements between vertebral and genetic identification methods.

		Vertebral Identity	
		<i>C. tilstoni</i>	<i>C. limbatus</i>
Genetic Identity	<i>C. tilstoni</i>	70	25
	<i>C. limbatus</i>	3	91

Chapter 6. Age, growth, and reproductive biology of two commercially important sharks from the Great Barrier Reef World Heritage Area



Plate 6. Spot-tail shark, *Carcharhinus sorrah* (May 2009).

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6.1 INTRODUCTION

The waters surrounding northern Australia are home to a diverse and abundant elasmobranch fauna that includes many endemic species (Last and Stevens, 2009). Two of the most abundant species are the Australian blacktip shark, *Carcharhinus tilstoni* – Whitley, 1950, and the spot-tail shark, *Carcharhinus sorrah* – Müller 0026Henle, 1839 (Last and Stevens, 2009). Both are medium-sized sharks occupying relatively shallow waters (<150m) on the continental shelf (Compagno *et al.*, 2005). *Carcharhinus tilstoni*, which closely resembles the much more widely distributed common blacktip shark, *Carcharhinus limbatus*, is endemic to Australian waters while *C. sorrah* occurs throughout the Indo-West Pacific and the Indian Ocean (Compagno *et al.*, 2005). These species have been the principle component of a number of commercial shark fisheries operating in the waters off northern Australia and are utilised for their meat and fins (Bensley *et al.*, 2010) (Chapter 2).

6.1.1 Fishery exploitation

The history of the exploitation of Australia's northern shark resources is, like many fisheries involving elasmobranchs, patchy in its documentation. The most intensive fishing off northern Australia occurred during the early 1970s, prior to establishment of the Australian Exclusive Economic Zone (EEZ). During this time a Taiwanese net fishery potentially harvested up to 30,000 t.yr⁻¹ live weight of shark, tuna and mackerel in the waters between northern Australia and Papua New Guinea (Walter, 1981). Following the establishment of the EEZ in 1979 a catch quota of 10,000 t.yr⁻¹ live weight was set by the Australian government, but by 1986 further gear restrictions and declining catch-per-unit-effort rendered the fishery uneconomically viable (Stevens and Davenport, 1991). *Carcharhinus sorrah* and *C. tilstoni* made up approximately 83% of the total shark catch within this fishery (Stevens and Wiley, 1986). Since the end of Taiwanese exploitation, sharks have been taken in smaller numbers (2000-3000 t.yr⁻¹) by a variety of fisheries operating off northern Australia both as target and by-catch (Bensley *et al.*, 2010). Presently, there is also an unknown but potentially high level of illegal, unregulated and unreported targeting of sharks for their fins off northern Australia (Field *et al.*, 2009). In the location of the present study, the Great Barrier Reef World Heritage Area (GBRWHA) off north-eastern Australia, *C. tilstoni* and *C. sorrah* make up approximately 50% of the shark catch by weight in a commercial net fishery (Chapter 2).

6.1.2 Current state of knowledge

Interest in the exploitation of Australia's northern shark resources, combined with concerns over the sustainability of the Taiwanese fishery, culminated in extensive study of the biology of *C. sorrah* and *C. tilstoni* during the late 1980s (Stevens and Wiley, 1986; Davenport and Stevens, 1988; Lavery and Shaklee, 1989; Stevens *et al.*, 2000b). The two species have similar life histories; maturity was attained relatively young (< 4 years), reproduction was by mode of placental viviparity, and the periodicity of reproduction was annual and almost identical in timing. Vertebral age and growth studies suggested both species were relatively short lived; *C. tilstoni* to around 12 years of age and *C. sorrah* to around seven years. However, recaptures following an extensive tagging study proved the maximum age of *C. tilstoni* is at least 18 and the maximum age of *C. sorrah* is at least 9 (Stevens *et al.*, 2000b; Last and Stevens, 2009). Based on these studies *C. tilstoni* and *C. sorrah* were perceived as comparatively productive shark species and capable of sustaining moderate levels of fishing.

Early research into the life history of *C. tilstoni* and *C. sorrah* has served as the benchmark for managing these species throughout all of northern Australia during the past 25 years. Despite being well studied in the past, research on the biology of these species has not been ongoing, nor has it extended beyond the Arafura Sea, the location of the original study. Consequently, management of these species across northern Australia cannot take into account potential spatial or temporal variation in life history characteristics. Spatial variation is well documented in shark populations and may extend to many facets of life history including growth, weight, maturity, fecundity, and timing and frequency of reproduction (Yamaguchi *et al.*, 2000; Walker, 2007). The vast area these species occupy over northern Australia spans at least 18° of latitude and 40° of longitude, offering ample space for such variation to occur. Temporal differences are somewhat less well documented in sharks but have been observed, especially in response to exploitation (Sminkey and Musick, 1995; Walker, 2007; Taylor and Gallucci, 2009). The previous study of *C. tilstoni* and *C. sorrah* was during the historically most intense period of fishing off northern Australia when both species were probably overexploited (Stevens and Davenport, 1991). The effect that such high levels of fishing may have had on the biology of these species is unknown.

6.1.3 Aims

After a 25-year hiatus since the first studies of the life histories of these species, we revisit the biology of Australia's two most commercially important tropical shark species. For the first time, we examine the age, growth and reproductive characteristics of *C. sorrah* and *C. tilstoni* within the GBRWHA, where they are subjected to the conflicting demands of commercial fishing and conservation. Specifically, we provide the first statistically derived estimates of length and age at maturity and maternity, and the fecundity at length relationships for these species in Australian waters. We also establish growth rates and compare the results with those from the previous study of these species. Finally we examine the reproductive strategies used by *C. tilstoni* and *C. sorrah* through a quantitative analysis of embryonic growth.

6.2 METHODS

6.2.1 Sample collection and species identification

Biological samples were collected between May 2007 and November 2010 from fishery-dependent sources along the east coast of Queensland from Princess Charlotte Bay (13°S) to Moreton Bay (27°S). The majority of samples were obtained from a fishery observer program monitoring the commercial gillnet sector of the Queensland East Coast Inshore Finfish Fishery (ECIFF) (Chapter 2), in the inshore waters (<25 m depth) of the GBRWHA which is between 13°S and 24°S. Additional samples were also purchased or donated by commercial and recreational fishers. Further samples were collected opportunistically during fishery-independent sampling activities carried out by the James Cook University Fishing & Fisheries Research Centre using multi-hook research longlines, gillnets and rod and reel. Shark length was measured as stretched total length (STL) in millimetres (mm) following Compagno (1984): the animal was placed ventral side down and the upper lobe of the caudal fin depressed in line with the body axis. Additional measurements of fork length (FL), and pre-caudal length (PCL) were recorded for a subsample of animals.

In the waters off northern Australia, *C. tilstoni* occurs sympatrically with *C. limbatus*, from which it is visually indistinguishable (Last and Stevens, 2009). These species can be separately identified using vertebral counts, molecular techniques, and by their life history characteristics at certain life stages. In the present study we observed discrepancies in species identification depending on which method was used. It was therefore necessary to establish a

protocol to minimise misidentification of these species. The protocol, based on Chapter 5, was used to identify *C. tilstoni* and is provided in Appendix 1.

6.2.2 Vertebral processing and growth analysis

A section of five vertebrae was removed from the anterior region of the vertebral column between the gills and the first dorsal fin and stored frozen. A scalpel was used to remove the neural and haemal arches and soft tissue leaving only the vertebral centra. Centra were then soaked in a solution of 5% sodium hypochlorite (bleach) for approximately 30 minutes to remove remaining tissue, then rinsed thoroughly under tap water, and placed in a drying oven at 60°C for 24 hours. One of the five centra prepared from each individual was selected for ageing. A single 400–600 µm longitudinal section was taken through the focus of the centrum using a slow-speed saw with a diamond-tipped blade (Beuhler, Illinois, USA) (Cailliet and Goldman, 2004). Centra <10 mm in diameter were cast in a clear polyester resin prior to sectioning as they were too small to fit in the vice of the saw. The vertebral section was fixed to a glass slide using Crystal Bond adhesive (SPI Supplies, Pennsylvania, USA).

Sectioned centra were examined under a dissecting microscope using transmitted light. The age of an animal was determined by counting the pairs of opaque and translucent (hyper- and hypomineralised) growth bands deposited on the corpus calcareum (Cailliet and Goldman, 2004). The birth mark was identifiable by a change of angle on the corpus calcareum. Since both species have seasonal reproductive cycles, it was possible to assign partial ages to all individuals using a mean population birth date of December 1st (assigned on the basis of reproductive data below). Davenport and Stevens (1988) previously validated that growth bands pairs are formed annually in *C. tilstoni* and that growth bands are formed approximately a year after birth. As such the first growth increment was also assumed to be 1 year for both species. Prior to ageing all centra, a random sub-sample was read by two readers to ensure that a consensus was reached regarding interpretation of the banding pattern, then one of the readers read all of the centra twice. Precision between reads was evaluated using Chang's (1982) method of the coefficient of variation (CV) and percent agreement following the method of Goldman and Musick (2006). Bias between reads was evaluated statistically using Bowker's test of symmetry (Evans and Hoenig, 1998).

An information theoretic, multi-model inference (MMI) approach was taken to modelling growth (Burnham and Anderson, 2001). This approach has been proposed as an improvement to a

priori fitting of the von Bertalanffy growth model and provides a framework for making inferences based on more than one model (Katsanevakis and Maravelias, 2008). A set of six candidate models was developed and fit to length-at-age data (Table 6.1). These consisted of three parameter versions of the von Bertalanffy (VB3) and Gompertz (GOM3) growth curves, as well as two parameter versions of these models (VB2 and GOM2) incorporating known lengths-at-birth. Length-at-birth established from the present study was 619 mm for *C. tilstoni* and 550 mm for *C. sorrah*. A logistic growth function and a two phase version of the von Bertalanffy growth model (TPVB) were also considered (Soriano *et al.*, 1992; Thorson and Simpfendorfer, 2009). Each model represented an alternative hypothesis for growth, and all models assumed growth was asymptotic (Table 6.1).

Models were fit using the method of nonlinear least squares in the statistical package R (R Development Core Team, 2009) and model performance evaluated using Akaike's Information Criteria (AIC). The best model was the one with the lowest AIC value, AIC_{min} . AIC differences were calculated as $\Delta_i = AIC_i - AIC_{min}$, and used to rank the support of the remaining models ($i=1-6$) relative to the best model. Models with Δ of 0-2 had substantial support, while models with Δ of 4-7 had considerably less support. Models with $\Delta > 10$ had essentially no support (Burnham and Anderson, 2002). Akaike weights (w) were calculated as the weight of evidence in favour of a model being the best model in the set of candidate models (Burnham and Anderson, 2002). Ninety-five percent confidence intervals around the best-fit parameter estimates and population estimates were derived from 10,000 re-sampled datasets using the bias-corrected accelerated bootstrap method (Efron and Tibshirani, 1993).

6.2.3 Age validation

Davenport and Stevens (1988) previously validated annual growth band pair deposition in *C. tilstoni* using oxytetracycline (OTC). In that study *C. sorrah* were also injected with OTC although only one successful recapture was made after 199 days at liberty. In addition to validation, annual band pair formation was verified for both species using size-mode analysis and tag recapture data (Stevens *et al.*, 2000b). Although Davenport and Stevens (1988) verified that growth bands were formed annually in *C. sorrah*, we attempted to validate this hypothesis using a mark, tag and recapture study in the waters of Cleveland Bay (19°12'S, 146°54'E) near Townsville. The lengths and sex of captured sharks were recorded and individuals were then tagged externally on the first dorsal fin using Rototags or Jumbotags (Dalton, Worldwide). The

vertebral centra of captured sharks were marked using the fluorescent dye calcein ($C_{30}H_{26}N_2O_{13}$). A pH-buffered, isotonic solution of 12.5 mg.mL^{-1} calcein was injected intramuscularly behind the first dorsal fin at a dosage of 5 mg.kg^{-1} (McAuley *et al.*, 2006).

6.2.4 Reproductive biology

Quantitative analysis of reproductive biology closely followed the format outlined in Walker (2005b) that has also been adopted by Braccini *et al.* (2006), Huveneers *et al.* (2007), Walker (2007) and Trinnie *et al.* (2009).

6.2.5 Length-weight relationship

The relationship between total body mass, W , and STL, l , was determined using a power curve: $W(l) = \beta_1 l^{\beta_2}$ where β_1 and β_2 are fitted parameters estimated using linear regression analysis: $\ln(W(l)) = \ln(\beta_1) + \beta_2 \ln(l)$. Sex and the interaction of sex and STL were included as a factor in the linear model to establish whether there was a difference in weight-at-length between males and females. The maximal model including all parameters was fitted and the best model obtained through backward step-wise elimination of non-significant parameters.

6.2.6 Maturity and maternity analysis

A single index was adopted for staging maturity in each sex, based on the descriptions of Walker (2005b) (Table 6.2). Maturity stage of males was based on clasper condition ($C = 1-3$), while maturity stage of females was based on uterus condition ($U = 1-6$). Maturity stage data was converted to binary form (immature = 0, mature = 1) for statistical analysis. Population estimates of length-at-maturity were established using a logistic regression model (Roa *et al.*, 1999) that was re-formulated following Walker (2005b):

$$P(l) = P_{MAX} \cdot \left(1 + e^{-\ln(19) \left(\frac{l - \beta_1}{\beta_2 - \beta_1} \right)} \right)^{-1},$$

where $P(l)$ is proportion of the population mature at STL, l , where β_1 and β_2 are fitted parameters corresponding to l_{50} and l_{95} respectively, and P_{MAX} is the asymptote, fixed at 1 in all analyses. A generalised linear model (GLM) with a binomial error structure and logit link function was used to estimate parameters β_1 and β_2 . The effect of sex on length-at-maturity was examined by including sex and the sex-STL interaction as terms in the GLM. Non-significant terms were removed through backward step-wise elimination and χ^2 tests used to test the hypotheses that sex

and the sex-STL interaction had a significant effect on length-at-maturity. Population estimates of age-at-maturity and length- and age-at-maternity were also established using this method. A female was classed as in maternal condition if it would have given birth during December of the year it was caught. This included all females with $U = 4 - 6$. Female *C. sorrah* for which the largest follicle diameter (LFD) in the ovary was > 10 mm between January and March were also classed as in maternal condition, as they would have become pregnant and given birth that year. Female *C. tilstoni* with LFD > 15 mm between January and March were also classed as in maternal condition for this reason.

6.2.7 Fecundity and embryonic sex ratio

The relationship between fecundity, F , and maternal STL, l , was established using a linear regression model: $F(l) = \beta_1 + \beta_2 l$, where β_1 and β_2 are fitted parameters. A χ^2 test was used to test whether the sex ratio of all *in utero* embryos was significantly different from 1:1.

6.2.8 Timing of reproduction and embryonic growth analysis

The timing of the ovarian cycle was determined by examining the ovary of mature females ($U = 3 - 6$ animals) and measuring the diameter of the largest follicles (LFD) in millimetres. LFD was then plotted against month. To examine patterns of growth in embryos, the mean STL of embryos from pregnant females ($U = 4$ and 5 animals) was modelled as a function of age. Where embryos were not yet macroscopically visible ($U = 4$ animals), the STL of embryos was taken as 0. The age of developing embryos was estimated from the time since conception, based on examination of $U = 3$ and 4 animals between January and April. Growth was clearly not constant throughout the gestation period and appeared to be influenced by season. As such, the Hoenig and Hanumara variation of the von Bertalanffy growth function, which incorporates seasonal fluctuations in growth, was used to model embryonic growth (Pawlak and Hanumara, 1991):

$$L(t) = \beta_1 - \beta_1 e^X, X = -\beta_2(t - \beta_3) - \frac{\beta_2\beta_4}{2\pi} \sin 2\pi(t - \beta_5) + \frac{\beta_2\beta_4}{2\pi} \sin 2\pi(\beta_3 - \beta_5),$$

where L is STL in mm, t is time in years, β_1 is asymptotic length (L_∞) in mm, β_2 is the Brody growth coefficient K in years⁻¹, β_3 is t_0 in years, β_4 is the magnitude of oscillations in growth, and β_5 is the age at which zero growth begins. Length-at-birth was established based on the length of the largest *in utero* embryos or from measurement of neonates, which were identifiable by the presence of an unhealed umbilical scar. The relationship between total body mass (kg) and STL for *in utero* embryos was established as described for post-natal animals above.

6.3 RESULTS

6.3.1 Sample collection and species identification

Samples were obtained from a total of 656 *C. sorrah* consisting of 345 males, 545 – 1138 mm, and 311 females, 550 – 1310 mm (Figure 6.1 a). The relationships between STL, fork length (FL) and pre-caudal length (PCL) for a subsample of individuals for sexes combined were:

$$STL = 105.5 + 1.135 \cdot FL \quad (r^2 = 0.97, p < 0.01, \text{d.f.} = 488)$$

$$STL = 91.93 + 1.275 \cdot PCL \quad (r^2 = 0.98, p < 0.01, \text{d.f.} = 239)$$

Samples were obtained from a total of 1003 ‘unidentified’ blacktip sharks, consisting of both *C. tilstoni* and *C. limbatus*. Using the identification protocol provided in Appendix 1 a total of 479 individuals were identified as *C. tilstoni*, consisting of 240 males, 555 – 1560 mm, and 239 females 570 – 1800 mm (Figure 6.1 b). The relationships between STL, FL and PCL for a subsample of individuals for sexes combined were:

$$STL = 35.03 + 1.214 \cdot FL \quad (r^2 = 0.99, p < 0.01, \text{d.f.} = 429)$$

$$STL = 22.79 + 1.359 \cdot PCL \quad (r^2 = 0.99, p < 0.01, \text{d.f.} = 275).$$

6.3.2 Age validation

One hundred and thirty four *C. sorrah* were marked with calcein and released, of which six individuals were recaptured after between 188 and 452 days at liberty (Table 6.3). All recaptures were of large (>1000 mm) females, five of which were pregnant and had shrunk in length when measured in the laboratory. While this was likely a result of measurement error during initial tagging it suggested that minimal growth had occurred since they were originally tagged. Uptake of calcein on the vertebrae was poor, with a mark visible on only two individuals. Individual 3, at liberty for 359 days had a faint mark visible on the outer margin of the vertebrae centra but due to the closeness of bands on the edge it was unclear if a band-pair had formed since being marked. Individual 4, released in October and at liberty for 241 days, had a narrow translucent band closely following the calcein mark and had formed a wide opaque band after it. This supports the hypothesis that a single translucent band is formed during early summer, and a wide opaque band formed throughout the rest of the year. Although we were unable to conclusively validate that growth bands pairs are annual in *C. sorrah*, given the strong support

from modal analysis and tag recapture data provided by Davenport and Stevens (1988), we assumed that, like *C. tilstoni*, translucent bands are formed during early summer and that band-pair formation was an annual occurrence throughout life.

6.3.3 Precision and bias in age estimation

Mean percent agreement (PA) and $PA \pm 1$ year between the first and second read pooled into 100 mm length groupings was 68% and 79% for *C. sorrah*, while Chang's coefficient of variation (CV) was 14.77%. There was a highly significant difference between the first and second reads (Bowker's Test of Symmetry: $\chi^2 = 38.75$, d.f. = 19, $p < 0.01$); individuals up to five years old were aged consistently between reads but there was systematic over-ageing of those older than five (Figure 6.2 a). For *C. tilstoni*, mean PA and $PA \pm 1$ year between the first and second read pooled into 100 mm length groupings was 60% and 72%, while Chang's coefficient of variation (CV) was 22.02%. Again, there was a highly significant difference between the first and second read (Bowker's Test of Symmetry: $\chi^2 = 63.32$, d.f. = 26, $p < 0.01$); individuals up to six years old were aged consistently between reads but there was systematic under-ageing of those older than six (Figure 6.2 b). For both species, ageing of younger animals was consistent between reads and, despite being statistically significant, the magnitude of bias on older individuals was relatively low. As such, the second read was considered an acceptable interpretation and used as the final age in both cases.

6.3.4 Vertebral growth analysis

Vertebrae centra were obtained and read from 294 *C. sorrah* consisting of 151 males, 545–1120 mm, and 143 females, 550–1301 mm. The youngest male and female were zero (both had unhealed umbilical scars) and were 545 and 550 mm. The oldest male was 8.9 years old and 1009 mm and the oldest female was 13.7 years old and 1310 mm. Both sexes of *C. sorrah* displayed strongly asymptotic growth, with growth rates fast during the first few years of life but rapidly slowing thereafter (Figure 6.3 a–c, Table 6.4), especially in males. The logistic model was the most parsimonious for males in the multi-model analysis of growth (Table 6.4, $w = 69.48\%$). The GOM3 model was also supported by the data to some extent (Table 6.4, $\Delta = 2.21$, $w = 23.06\%$), while the other models had little support. Growth to asymptotic size occurred at a slower rate for females and the VB2 model was the best given the data (Table 6.4, $w = 43.74\%$). The TPVB and VB3 models were also supported by the data (Table 6.4, $\Delta < 2$, $w > 20\%$). Male and female growth was similar in individuals younger than two years of age and the slight difference between

growth curves was probably due to a deficiency of the data, as few very small females (< 650 mm) were sampled compared to males. At approximately two years of age, growth became sexually dimorphic; male growth effectively ceased while females continued to grow (albeit at a much slower rate) for the remainder of their lives.

Vertebrae centra were obtained and read from 429 *C. tilstoni* consisting of 201 males, 585 – 1590 mm, and 228 females, 593 – 1800 mm. The youngest male and female were zero (both had unhealed umbilical scars indicating recent birth), and were 585 mm and 593 mm. The oldest male was 12.8 years and 1540 mm and the oldest female was 14.8 years and 1800 mm. Length-at-age-data fit to the candidate model showed strong support for two-phase growth for both sexes (Figure 6.3 d – f, Table 6.4). For both males and females the TPVB model was convincingly the best given the data ($w > 90\%$), and explained much more of the variance compared to the competing models, all of which had negligible support (Table 6.4, $w < 5\%$). A comparison of the male and female curves (Figure 6.3 f) showed that growth was virtually identical between sexes until approximately 4 years of age, after which point there was a brief slowing and cessation of growth. This occurred at 4.1 years in males and 4.7 years in females (parameter β_5). After growth resumed, growth rates were similar between sexes although females attained a larger length than males. A pronounced asymptote was not observed for either sex.

6.3.5 Length-weight relationship

Weight-at-length data were available for 189 *C. sorrah*. The largest male weighed 8.10 kg (1139 mm), while the largest female was 14.45 kg (1260 mm). Although there was a large difference in maximum weight between males and females, neither sex, nor the sex-length interaction was significant and removal of these terms did not result in a significantly worse fit of the model to the data ($F = 0.7721$, $d.f. = 2$ and 187 , $p = 0.4635$). Step-wise backward elimination of these parameters resulted in a single slope and intercept for both sexes (Figure 6.4 a). Weight-at-length data were available for 176 *C. tilstoni*. The largest male weighed 20.85 kg (1485 mm), while the largest female was 34.15 kg (1660 mm). Like *C. sorrah*, there was a weak effect of sex on the length-weight relationship and neither sex nor the sex-length interaction was significant. Step-wise backward removal of these terms did not significantly decrease the explanatory power of the model ($F = 1.743$, $d.f. = 2$ and 174 , $p = 0.178$) and as such the final model contained a single intercept and slope for both sexes (Figure 6.4 b)

6.3.6 Maturity and maternity ogives

Sufficient data were obtained from staging male clasper condition and female uterus condition in *C. sorrah* and *C. tilstoni* to construct length- and age-at-maturity ogives for both sexes, and length- and age-at-maternity ogives for females (Table 6.5 and Table 6.6, Figure 6.5). In both species, maturity was attained at a similar length and age between sexes. In the GLM analysis for *C. sorrah* neither sex nor its interaction explained a significant amount of the variance, thus rejecting the hypotheses that these factors had a statistically significant effect on when maturity occurred (Table 6.7, Figure 6.5 a–f). Length-at-50% maturity for both sexes was 933 mm and age-at-50%-maturity was 2.3 years (Figure 6.5). Maternity ogives were to the right of maturity ogives and females generally became pregnant in the year following maturation; length-at-50%-maternity was 1029 mm and age-at-50%-maternity was 3.4 years.

Similar trends were found in the GLM analysis for *C. tilstoni* (Table 6.7), with neither sex nor its interaction significant, thus rejecting the hypotheses that these factors had a statistically significant effect on maturity. Length-at-50% maturity for both sexes was 1208 mm and age-at-50% maturity was 5.5 years in both sexes. Females appear to become pregnant one to two years after maturity; length-at-50%-maternity was 1374 mm and age-at-50% maternity was 7.5 years. The relatively small number of females in maternal condition led to greater uncertainty around parameter estimates for maternity ogives in *C. tilstoni*. This is reflected in the wider confidence intervals for these analyses. All ogives including those modelling maternal condition were highly significant (Figure 6.5).

6.3.7 Fecundity and sex ratio

Macroscopically visible *in utero* embryos were examined from 71 pregnant (U = 5) *C. sorrah*, 1010 – 1301 mm STL. The litter size of U = 5 animals ranged from 1–6 with a mean (\pm sd) of 3.042 (\pm 0.985). The only U = 4 pregnant female examined had 3 *in utero* eggs. There was a significant linear relationship between increasing maternal STL and fecundity (Figure 6.6 a), such that the largest individuals were the most fecund. Of 161 embryos from 52 litters where the sex could be established for all individuals, 75 were females and 86 were males. The sex ratio of embryos was not significantly different from 1:1 ($\chi^2 = 0.7516$, *d.f.* = 1, *p* = 0.386). Macroscopically visible *in utero* embryos were examined from 22 pregnant *C. tilstoni*, 1410 – 1800 mm. The litter size of U = 5 animals ranged from 1–7 with a mean of 3.818 (\pm 1.259). No U = 4 pregnant females were examined. Like *C. sorrah*, there was a significant linear relationship

between increasing maternal STL and fecundity (Figure 6.6 b). Of 38 embryos obtained from 10 litters, 24 were male and 14 were female. Although there was a bias toward males in the sample, it was not statistically significant due to the low sample size ($\chi^2 = 2.631$, $d.f. = 1$, $p = 0.1048$). The mean (\pm s.d.) proportion of females per litter was 0.36 ± 0.21 and ranged from 0 to 0.75.

6.3.8 Timing of reproduction and embryonic growth analysis

The timing and periodicity of the ovarian cycle of *C. sorrah* was established from examining the ovarian follicles of 75 mature females during nine months of the year and consisting of 10 U = 3 animals, one U = 4 animal, 61 U = 5 animals and three U = 6 animals (Figure 6.7 a). The LFD of mature individuals ranged from 3 – 30 mm. Although *C. sorrah* has an annual reproductive cycle, follicle development did not occur synchronously with the gestation period. As such, ovulation did not coincide with parturition. Between May and October follicle growth was negligible, increasing from a mean of 5 mm to 7.5 mm. Follicle growth increased after October, however the mean LFD of three U = 6 females examined in December was still only 10.33 mm, approximately 30% of the diameter of the largest post-ovulatory follicle measured in a U = 5 female in April. Although no mature females were examined between January and March it is evident that the majority of follicle growth and yolk accumulation occurs after December. Based on the examination of U = 5 females in early April (day 92) it appears that, for the majority of the population, ovulation occurs during mid March and that the diameter of mature follicles is approximately 25 – 30 mm (Figure 6.7 a). A single U = 4 female examined during early April (day 100) appeared to be an outlier.

The timing and periodicity of the ovarian cycle of *C. tilstoni* was difficult to infer as follicles were measured in only 18 mature females from five months of the year (five U = 3 females, 11 U = 5 females and two U = 6 females) (Figure 6.7 b). The ovarian cycle in *C. tilstoni* appears to commence earlier than *C. sorrah*; by late November (days 325 – 335) the mean LFD of 7 females (including two U = 6) was 17.4 mm, approximately 60% of the diameter of the largest pre-ovulatory follicle measured. Follicles had begun accumulating yolk in November, but were not mature, indicating parturition and ovulation are not synchronous. Based on the examination of a U = 3 female in mid March (day = 71) with pre-ovulatory follicles of 30 mm diameter it seems likely that ovulation occurs around this time. This is further supported by the examination of several U = 5 females in early April (days 91–94).

For *C. sorrah*, the timing and period of pregnancy was inferred from 66 U = 5 females, two U = 6 females and two neonates. Based on the assumption of mid-March ovulation (15th March, day 75) and the examination of U = 6 females and neonates in late November to mid-December (days 335, 348 and 354) suggests a period of pregnancy of approximately 260–279 days, or 9 months. Embryonic growth did not occur evenly throughout pregnancy and appeared to be influenced by seasonal fluctuations in temperature. This was captured in the Hoenig and Hanumara version of the von Bertalanffy growth model fit to the embryo length-at-age data (Figure 6.8 a). Growth rates were rapid at the beginning of the gestation period but slowed during winter months (July–September) (Figure 6.8 c). Embryonic growth rate was lowest in August, approximately a month after the lowest daily temperatures, and then increased with rising temperature until parturition. Length and weight of embryos increased throughout pregnancy to a length of at least 524 mm and weight of 0.689 kg (Figure 6.9 a) in late November (day 335). The lengths of two neonates with unhealed umbilical scars were 545 mm and 550 mm.

The timing and length of the period of pregnancy for *C. tilstoni* was inferred from 21 U = 5 females, two U = 6 females, and 44 neonates. The two U = 6 females were captured on days 325 and 335, while 44 neonates with unhealed umbilical scars were captured between day 305 (late October) and day 27 (late January). The vast majority of neonates, however, were caught during days 343–353 (early December). Therefore, while a small number of individuals may pup as early as October or as late as January, reproduction is strongly synchronous and most females appear to give birth in early December. Assuming ovulation occurs mid-March (March 15th, day 75) this suggests *C. tilstoni* has a period of pregnancy of around 268–278 days or approximately 9 months. Although based on less data (mean embryo lengths from 21 U = 5 females), seasonal fluctuations in embryonic development during pregnancy appear to be more pronounced for *C. tilstoni* (Figure 6.8 b). Like *C. sorrah*, embryonic growth rate was lowest during August, but rapidly increased with increasing temperature until parturition. The length and weight of embryos increased throughout pregnancy to between 578–644 mm and 1.25–1.55kg – the size range among two litters examined from U = 5 females on day 333 (Figure 6.9 b). The length of 44 neonates was 585–663 mm with a mean (\pm s.d.) of 621.6 ± 19.8 mm, while the mean weight of 15 neonates was 1.360 ± 0.198 kg.

6.4 DISCUSSION

This research was the most comprehensive study on the life history of *C. sorrah* and *C. tilstoni*, Australia's two most commercially important tropical sharks. It is also the first time the biology of these species has been studied in detail within the GBRWHA. The models of key life history processes presented are necessary for quantitative population assessments and should be used to inform management of these species across northern Australia. In contrast to the typical approach of publishing age-and-growth and reproductive biology separately, we present both simultaneously, allowing a comprehensive insight into these closely inter-related facets of life history. A synopsis of the major findings for each species is presented below and discussed in relation to previous results.

6.4.1 *Carcharhinus sorrah*

In general the findings of this study corroborate with those of Stevens and Wiley (1986) and Davenport and Stevens (1988) in the Arafura Sea and confirm that *C. sorrah* is a comparatively productive species throughout northern Australian waters. Growth after birth was rapid, and by age one both sexes had increased in length by approximately 37% to ~750 mm and increased in body mass by approximately 200% to ~2 kg. On average, both sexes reached maturity shortly after their second summer at a length of 933 mm and 2.3 years of age. It is important to recognise though, that as reproduction is strongly seasonal and mating and ovulation occur during summer, reproduction does not commence until the following summer and that neither sex reproduces until at least age three. Indeed this is reflected in maternity ogives for females (Figure 6.5 c and f), which indicate the age at 50% maternity is 3.4 years and that females therefore begin reproducing at 3 – 4 years old.

Growth curves for males and female *C. sorrah* were indistinguishable until maturity was reached, after which point they diverged and growth became strongly sexually dimorphic — a general feature of shark populations (Cortés, 2000). In comparison with previous studies, the female growth curve was visually indistinguishable to that found by Davenport and Stevens (1988) who reported k and L_{∞} values of 0.34 and 1239 mm, compared with values of 0.3389 and 1265 mm obtained in the present study (Figure 6.10 b). Stevens and Wiley (1986) did not statistically model length at maturity or maternity but stated that between 950 and 1000mm, 50% of females were pregnant. This suggests that in the Arafura Sea, *C. sorrah* began reproducing at a slightly smaller length to the GBRHWA (1029 mm), but were probably not pregnant until at least

three years old either. Fecundity was also similar between studies; females produced an average of 3.042 pups per litter in the GBRWHA compared with 3.1 in the Arafura Sea. Stevens and Wiley (1986) also found that litter size increased with maternal length, but did not provide regression parameters so comparison of fecundity at length relationships was not possible.

In contrast to the similarities between females, the biology of males from the GBRWHA was slightly different to the Arafura Sea. Davenport and Stevens (1988) reported k and L_{∞} values of 1.17 and 984 mm compared with the values of 0.6419 and 1072 mm obtained from the VB3 model in the present study. This indicates male *C. sorrah* in the Arafura Sea grew faster and to a smaller maximum length, and as such were probably capable of reproducing as young as two years old. In both studies, male growth was characterised by a rapid slowing and almost complete cessation of growth after maturity. As such the models that best described male growth were the logistic and the GOM3 models both of which allowed for non-linear slowing of growth rate as length increased. Although a sigmoidal relationship between length and age is not commonly reported, logistic growth models have previously been fitted to length-at-age data for elasmobranchs (McFarlane and King, 2006; Romine *et al.*, 2006). For male *C. sorrah* the length-at-age relationship was clearly not sigmoidal and the point of inflection occurred at age 0. In this case the preference of the logistic model was apparently due to its greater flexibility compared to the other models such as the VB (itself an extension of the Verhulst logistic growth model (Tsoularis and Wallace, 2002)).

Though there are few other studies on the biology of *C. sorrah* for comparison, there is evidence to support interspecific variation in life history characteristics in populations outside Australia. Devadoss (1988) reported that females matured at 1200 mm and males at 1150 mm in the waters off India, close to the maximum length of *C. sorrah* in Australian waters. Devadoss (1988) also reported a biennial reproductive cycle compared with an annual cycle in Australian waters. In Indonesia, where *C. sorrah* populations are comprised of a genetically distinct stock to Australia (Ovenden *et al.*, 2009), White (2007) reported that males matured at 1117 mm, and that females attained a maximum length of at least 1572 mm and males at least 1278 mm. Other reports of *C. sorrah* in the Indian Ocean, albeit fragmentary, suggest a similar biology to the Indo-Pacific region (Bass *et al.*, 1975). Based on this, *C. sorrah* appears to have a much smaller length at maturity and usual size attained in Australian waters and as such, life history data from this region may be inappropriate for managing this species elsewhere in its range. This highlights the need for more studies of the life history of *C. sorrah* throughout the Indo Pacific region and

the Indian Ocean, especially given its commercial importance in some areas, e.g. Indonesia (Blaber *et al.*, 2009).

Validation of the vertebral growth band pattern was attempted for *C. sorrah* but was not possible due to a low recapture rate and failure of calcein to be absorbed by the vertebrae in four of the six recaptures. As all injected animals were mature (and mostly pregnant) females, we attribute this to the slow absolute growth rates of *C. sorrah* after maturity and during pregnancy. The vertebrae of other species captured as juveniles and injected with calcein during fishery-independent sampling were successfully marked e.g. *Sphyrna mokarran* (Chapter 4). This suggests that calcein may be ineffective as an age validation tool when injected in animals that are close to L_{∞} or allocating a large proportion of their energy into reproduction. In the absence of validation, recaptures by Stevens *et al.* (2000b), who tagged 2919 *C. sorrah*, confirm the longevity of this species. The mean STL of animals tagged in that study was 922 mm (~2 years old) (CSIRO Division of Marine and Atmospheric Research, 2009), implying that the age of the oldest recaptured animals (up to 9.9 years) was at least 12 years old. This agrees closely with the oldest animal aged in the present study (13.67 years) and provides strong evidence to suggest that growth band pairs are formed annually throughout life in *C. sorrah*, as they are in several other carcharhinid sharks (Davenport and Stevens, 1988; Simpfendorfer *et al.*, 2002b; McAuley *et al.*, 2006). The periodicity of the banding pattern and growth rates in younger *C. sorrah* was also clearly verified as annual by Davenport and Stevens (1988).

6.4.2 *Carcharhinus tilstoni*

The present study highlighted differences in the biology of *C. tilstoni* compared with previous studies in the Arafura Sea, particularly in age at maturity. In the GBRWHA, *C. tilstoni* matured at a slightly larger length ($l_{50} = 1208$ mm compared with approximately 1200 mm for females) and an older age ($a_{50} = 5.49$ years for females compared with 3 – 4 years) (Stevens and Wiley, 1986; Davenport and Stevens, 1988). At 1300 mm approximately 50% of females were pregnant in the Arafura Sea compared with a slightly larger 1374 mm in the GBRWHA. Most importantly, age at maternity in the present study was calculated as 7.45 years, implying that females probably do not begin reproducing until 7 – 8 years old, considerably older than surmised by Davenport and Stevens (1988). A higher mean fecundity was also found in the present study (3.8 compared with 3.0) however the fecundity at length relationship could not be compared between studies.

Under the information-theoretic, MMI analysis of growth, both sexes showed strong ($w > 90\%$) support for two-phase growth. Two-phase variants of the von Bertalanffy growth model have been proposed as alternative growth models for long-lived fish where changes in growth rate occur due to dietary or habitat shifts, or differences in energy allocation upon maturation (Soriano *et al.*, 1992; Day and Taylor, 1997). Support for two-phase growth has been found in a number of elasmobranchs (Braccini *et al.*, 2007; Tribuzio *et al.*, 2010), with decreases in growth rate typically occurring around the time of maturity, thus supporting the hypothesis of a shift in surplus energy allocation (Araya and Cubillos, 2006). Decreases in growth of *C. tilstoni* occurred at approximately 4.1 years in males and 4.5 years in females (parameter β_5 , Table 6.4) with the duration of decreased growth longer in females. This is slightly before a_{50} in both sexes (5.49 years), and may indicate a shift in energy allocation as maturity is reached.

Criticisms of the TPVB model are that such observations may be an artefact of sampling rather than actual biphasic growth (Soriano *et al.*, 1992). This is a valid concern and two-phase models should be used cautiously. For example, by virtue of its extra parameters the TPVB provided a better fit to the data ($w = 34.08\%$) than the VB3 model ($w = 21.31\%$) for female *C. sorrah*, despite no suggestion of two distinct phases of growth in this species. Also, although considerable effort was undertaken to remove the morphologically similar *C. limbatus* from our analyses, we also cannot conclusively rule out misidentification as a cause of the apparent two-phase growth. However, we feel the apparent prevalence of this phenomenon in elasmobranchs, including in studies with robust datasets (Braccini *et al.*, 2007; Tribuzio *et al.*, 2010), justified the inclusion of the TPVB in our set of candidate models along with the more conventionally used growth models (e.g. VB and GOM).

In comparison to previous ageing studies of *C. tilstoni* in the Arafura Sea, which used the standard VB model, growth curves from the present study were similar in trajectory (Figure 6.10 c and d). All male parameters common to both analyses were closely similar ($L_\infty = 1652$ mm, $k = 0.17$ yr⁻¹, $t_0 = -2.7$ yr, compared to $L_\infty = 1654$ mm, $k = 0.19$ yr⁻¹, $t_0 = -2.6$ yr, Figure 6.10 c), while females in the GBRWHA grew slower and to a larger length compared to the Arafura Sea ($L_\infty = 2046$ mm, $k = 0.11$ yr⁻¹, $t_0 = -3.39$ yr, compared to $L_\infty = 1942$ mm, $k = 0.14$ yr⁻¹, $t_0 = -2.6$ yr, Figure 6.10 d). Like *C. sorrah*, growth was similar between sexes until slightly before maturity was reached, after which point growth became sexually dimorphic with females attaining a larger length than males. Samples in the present study were representative of all length classes, allowing

accurate modelling of length at most ages. Despite this, all growth models poorly described the growth characteristics of the oldest animals in the population. This can be seen in the lack of a distinct asymptote. As such, asymptotic lengths exceeded the usual maximum length of this species (~1800 mm), especially in the VB models for females (e.g. L_{∞} for the best fit female TPVB model was 2046 mm).

A lack of distinct asymptote is a common feature of many shark growth curves (Simpfendorfer *et al.*, 2002b; McAuley *et al.*, 2006) and is generally considered an artefact of sampling; large (and old) sharks are rare or poorly sampled or they may have been removed from the population due to fishing. Some studies have also highlighted the increasing evidence to suggest that growth may not be asymptotic in some shark species (Bishop *et al.*, 2006; Braccini *et al.*, 2007). The majority of samples in the present study came from a fishery observer program monitoring a small-mesh gillnet fishery (Chapter 2). Samples were therefore biased toward smaller juveniles, potentially explaining the lack of observed asymptote in growth. However, the possibility that growth may not be asymptotic in some shark species should be investigated further and may warrant the development and use of non-asymptotic models.

Although sexes were obtained from complete litters of only 10 pregnant females there was a strong (but not statistically significant) bias towards males. Stevens and Wiley (1986) examined 734 *C. tilstoni* embryos and found a statistically significant bias towards males (53.8% of embryos male). While the embryonic sex ratio of shark is typically 1:1, biased sex ratios have been reported in a number of shark species. Among carcharhinids, however, this bias has most commonly favoured females (Saidi *et al.*, 2005; Henderson *et al.*, 2006; McAuley *et al.*, 2007b). The existence of a male biased sex ratio will ultimately reduce the population productivity of *C. tilstoni* and therefore needs to be included in any quantitative population assessments. Until more data can be obtained for the east coast of Queensland, we recommend using the data of Stevens and Wiley (1986) who found the embryonic female to male sex ratio was 0.86:1.

6.4.3 Intraspecific differences; real or methodological?

The present study highlighted a number of intraspecific differences between GBRWHA and Arafura Sea populations of these species, although establishing whether these are real or methodological is difficult without the raw data. One of the biggest differences was longevity. Based on vertebral age estimates, animals from the present study were considerably older:

C. sorrah males and females were aged to 5 and 7 years in the Arafura Sea, compared with 8.9 and 13.7 years in the GBRHWA, while *C. tilstoni* males and females were aged to 8 and 12 years compared with 12.8 and 14.8 years. As long-term tagging data indicated that these species live longer than this in the Arafura Sea (Stevens *et al.*, 2000b), differences in age structures between regions may be methodological. Davenport and Stevens (1988) aged vertebrae whole rather than sectioned, and this potentially contributed to under-ageing of animals. Growth overfishing also may account for the younger ages found by Davenport and Stevens (1988) given the intense level of commercial fishing in the Arafura Sea preceding that study. Not only are historical fishing levels much lower in the GBRWHA, but some samples (particularly adult female *C. sorrah*) were collected from areas closed to commercial fishing, potentially explaining why they were so much older.

Differences in maturity, particularly age at maturity, seem to be both methodological and real. For example, the age at maturity of 3 – 4 years for *C. tilstoni* stated by Davenport and Stevens (1988) was apparently converted from length at first maturity, as opposed to the modelling of A_{50} directly using maturity ogives (Walker, 2005b). This highlights the importance of modelling both maturity and maternity, however, it is insufficient to explain the large difference between maternity alone. For example, based on an approximate 50% maternity of 1300 mm by Stevens and Wiley (1986), *C. tilstoni* would have begun reproducing from 5–6 years of age in the Arafura Sea, compared to 7 – 8 years in the GBRWHA. We propose three hypotheses for the observed differences:

1. Temporal differences: intense fishing prior to study of *C. sorrah* and *C. tilstoni* in the Arafura Sea resulted in density-dependent changes in life history traits, most observable in a reduction in age at maturity.
2. Spatial differences: there may be naturally occurring intraspecific geographic differences in life history between populations, especially given the wide area these species occupy over northern Australia
3. Increased competition: greatly increased relative abundance of *C. limbatus* across northern Australia compared with the 1980s (Ovenden *et al.*, 2010) may have resulted in increased competition and caused changes in life history parameters of *C. tilstoni*.

We conclude that methodological differences are insufficient to explain all of the differences in life history found between the Arafura Sea and GBRWHA. The first two hypotheses above seem likely and are probably confounded. Both are well supported by examples in the literature e.g., Walker (2007).

The third hypothesis is more speculative. Ovenden *et al.* (2010) recently reported that *C. tilstoni* occurred in approximately equal frequencies to *C. limbatus* across northern Australia, in stark contrast to the ratio of 300:1 estimated by Stevens and Wiley (1986). *Carcharhinus limbatus* is also more prevalent at higher latitudes in Australian waters (Last and Stevens, 2009). As such on the east coast of Queensland there is a gradient of increasing *C. limbatus* abundance with latitude (Welch *et al.*, 2010). Combined with the recent finding of hybridisation between *C. tilstoni* and *C. limbatus* (Morgan *et al.*, In review), these factors, while still poorly understood, may contribute to the differences in life history observed between the Arafura Sea and GBRWHA. Irrespective of the causes, the findings of the present study imply that *C. tilstoni* is less productive than previously thought, and the new data provided should be factored into management.

6.4.4 Reproductive strategy

Few studies have sought to model embryonic growth specifically in elasmobranchs, yet our results demonstrate that this method can provide useful insights into reproductive strategy. Embryonic growth rate, like most aspects of physiology, was dependent on ambient environmental temperature — as has previously been observed in elasmobranchs (Harris, 1952; Wourms, 1977). Both *C. sorrah* and *C. tilstoni* employed a similar reproductive strategy: ovulation occurred during March and initial embryonic growth was rapid, but decreased to a minimum during winter. There was a lag of approximately one month between the lowest temperatures and the lowest embryonic growth rates. Following winter, growth rates increased with increasing temperature and birth occurred at the start of summer.

The comparison of embryonic growth rate with environmental temperature highlights the apparent advantages of this reproductive strategy. Neonates are born at the beginning of summer, presumably at the time of both highest food availability and capacity for growth. The majority of ovarian follicle growth then occurs during summer after the birth of pups, allowing the ovarian cycle to be shortened to approximately three months, while the total period of pregnancy

(ovulation, gestation and parturition) is approximately nine months. Among the inshore, tropical shark assemblage across northern Australia this reproductive strategy (with slight variations in timing) is also used by a number of similar size species including *Carcharhinus amblyrhynchoides* (Stevens and McLoughlin, 1991), *Carcharhinus fitzroyensis* (Lyle, 1987), and *Eusphyra blochii* (Stevens and Lyle, 1989). Few, if any, species greater in size than *C. tilstoni* seem to be capable of maintaining an annual reproductive cycle, suggesting it may be too energetically demanding for sharks larger than ~2m.

In the absence of an annual cycle, the most commonly used reproductive strategy appears to involve biennial reproduction with concurrent periods of pregnancy and ovulation lasting 12 months each and with parturition occurring during summer. Among the tropical northern Australia shark assemblage, this strategy is used almost exclusively by sharks >2 m in size, such as *C. plumbeus* (McAuley *et al.*, 2007b) and *S. mokarran* (Stevens and Lyle, 1989). Some, moderate sized annually reproducing tropical species such as *C. cautus* (White *et al.*, 2002) and *C. melanopterus* (A. Chin, personal communication) also switch to this biennial strategy at higher latitudes towards the southern extent of their range. Smaller species such as *Rhizoprionodon taylori* also use an annual cycle that is closely related to environmental temperature (Simpfendorfer, 1992b), although many such as *C. dussumieri* and *R. acutus* utilise an asynchronous strategy suggesting they are less dependent on temperature (Stevens and McLoughlin, 1991). Interestingly, Australia's two hemigalid species appear to use unique strategies altogether. *Hemigaleus australiensis* reproduces biannually, while the biennially reproducing *Hemipristis elongata* apparently ovulates in October and gives birth in April, such that the entire pregnancy period occurs during the period of highest temperatures and therefore is reduced to only 7 – 8 months in duration (Stevens and McLoughlin, 1991).

6.5 CONCLUSION

Sixteen summary points from this chapter are presented below:

1. Vertebral ageing methods gave longevity estimates of 9 and 14 years for male and female *C. sorrah* and 13 and 15 years for male and female *C. tilstoni*. These estimates are much higher than a previous ageing study that used whole rather than sectioned vertebrae, but are consistent with a previous tagging study, which recaptured *C. sorrah* after ~10 years at liberty and *C. tilstoni* after ~18 years.

2. A mark, tag and recapture study of *C. sorrah* using the fluorescent dye calcein was attempted to further validate age, but was unsuccessful due to failure of the calcein to mark the vertebrae. Most tagged animals were pregnant or close to their maximum size, and the failure of the calcein to mark the vertebrae may be due to the slow absolute growth rates of animals at this size.
3. Growth in both *C. sorrah* and *C. tilstoni* was sexually monomorphic prior to maturity, but became dimorphic after maturity.
4. Male *C. sorrah* attained a maximum length of 1138 mm and growth was best described by a logistic growth model due to the rapid and non-linear slowing of growth rate after maturity. Female *C. sorrah* attained a maximum length of 1310 mm and growth was best described by a standard von Bertalanffy growth function.
5. Male and female *C. tilstoni* attained maximum lengths of 1560 mm and 1800 mm, respectively. Strong support was found for two-phase growth in both species, with a cessation in growth occurring approximately a year before maturity.
6. The heaviest female *C. sorrah* (14.45 kg) was approximately 1.8 times greater in mass than the heaviest male (8.10 kg) and the heaviest female *C. tilstoni* (34.15 kg) was approximately 1.6 times greater in mass than the heaviest male (20.85 kg). Despite these differences, a single length-weight relationship with sexes combined was adequate for both species.
7. Bi-maturism was not observed in either species and both length- and age-at-maternity could be adequately described for both sexes using a single maturity ogive that was based on male clasper condition and female uterus condition.
8. Maturity ogives computed for *C. sorrah* ($l_{50} = 933.4$ mm and $a_{50} = 2.345$ years) implied that maturation occurred after the second summer and that individuals were therefore capable of reproducing by the beginning of the third summer (age three). Computed maternity ogives ($l_{50} = 1029$ mm and $a_{50} = 3.354$) confirmed this, indicating that females began reproducing at 3 – 4 years of age.
9. Maturity ogives computed for *C. tilstoni* ($l_{50} = 1208$ mm and $a_{50} = 5.491$ years) implied that most individuals matured between 5 – 6 years, while maternity ogives ($l_{50} = 1374$ mm and $a_{50} = 7.446$ years) indicate that females began reproducing one to two years after maturity at 7 – 8 years old.
10. Overall, growth curves were similar in shape to previous study of these species in the Arafura Sea but suggested slightly slower growth rates. Combined with slightly larger lengths at maturity, this resulted in older estimates for age at maturity, especially for

- C. tilstoni*. Methodological differences alone could not explain these differences. Historically high levels of fishing in the Arafura Sea compared with the GBRWHA and spatial differences are considered the most likely explanations. The apparent recent increase in relative abundance of *C. limbatus* across northern Australia may also have resulted in changes in the biology of *C. tilstoni* due to increased competition.
11. There was a significant linear relationship between maternal length and fecundity found for both species. The range of litter sizes observed was 1–6 for *C. sorrah* and 1–7 for *C. tilstoni*.
 12. The embryonic sex-ratio of neither species was significantly different from parity. However, in the small sample of *C. tilstoni*, there was a strong bias towards males. Based on previous studies, a slightly male-biased sex-ratio seems probable for this species, and this needs to be incorporated into population assessments.
 13. Both species had an annual, synchronous reproductive cycle of similar timing in the GBRWHA. Ovulation appeared to occur during March and parturition was during early December. As such, the period of pregnancy was approximately 9 months. The ovarian cycle did not occur synchronously with pregnancy, and, although not directly observed, the majority of follicle growth must occur in the months directly after birth.
 14. Embryonic growth rates were closely correlated with ambient environmental temperatures and embryonic development was slowest during winter. These species exploit environmental conditions so that parturition, mating and ovulation occur during summer, and thus enabling them to sustain an annual reproductive cycle.
 15. The largest *C. sorrah in utero* embryo measured was 524 mm and 0.689 kg, while the length of two free-swimming neonates was 545 and 550 mm. Forty-four neonate *C. tilstoni* measured had a mean length of 621.6 ± 19.8 mm and the mean weight of 15 was 1.360 ± 0.198 kg.
 16. The results of this paper provide the first statistically derived estimates of critical life history parameters (e.g. maturity and maternity) that are necessary to assist in quantitative population assessment and management. The biology of *C. tilstoni* is less productive in the GBRWHA than previously thought.

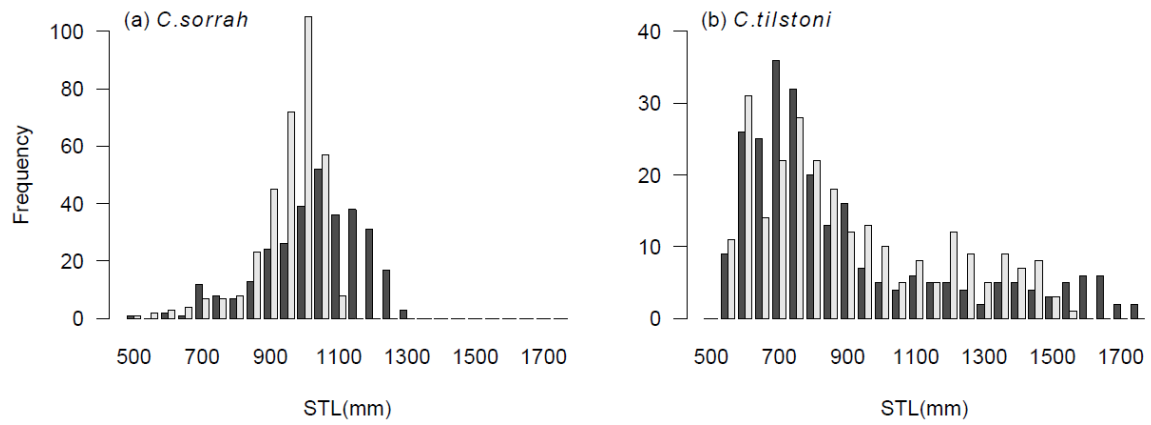


Figure 6.1 Length frequency distributions of male (light grey) and female (dark grey) samples used in the present study for *Carcharhinus sorrah* (a) and *C. tilstoni* (b).

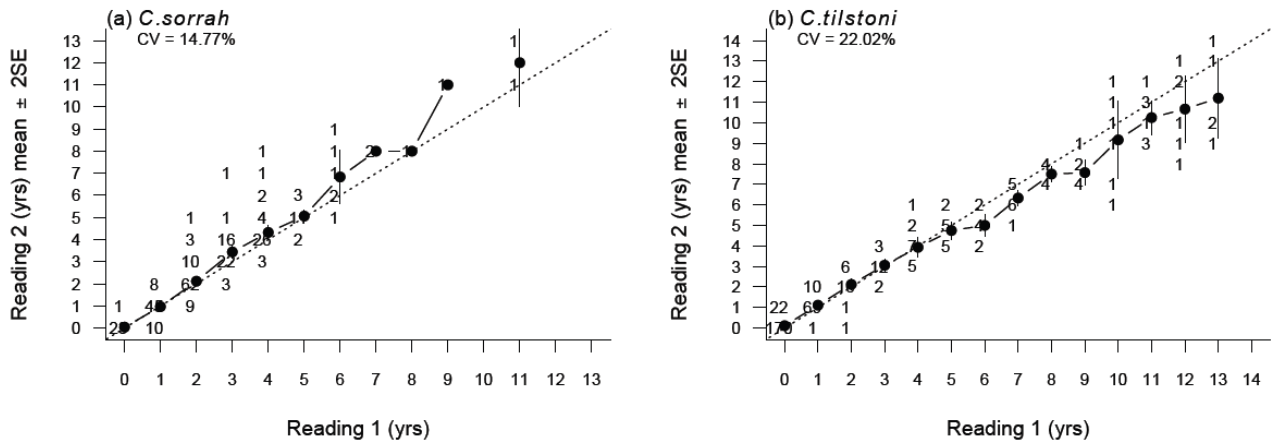


Figure 6.2 Intra-reader age-bias plots for *Carcharhinus sorrah* (a) and *C. tilstoni* (b) incorporating age-specific agreements used for Bowker's test of symmetry. Mean age-specific agreements ± 2 standard errors (\bullet) are plotted alongside the 1-1 equivalence line for comparison (---). CV is Chang's coefficient of variation.

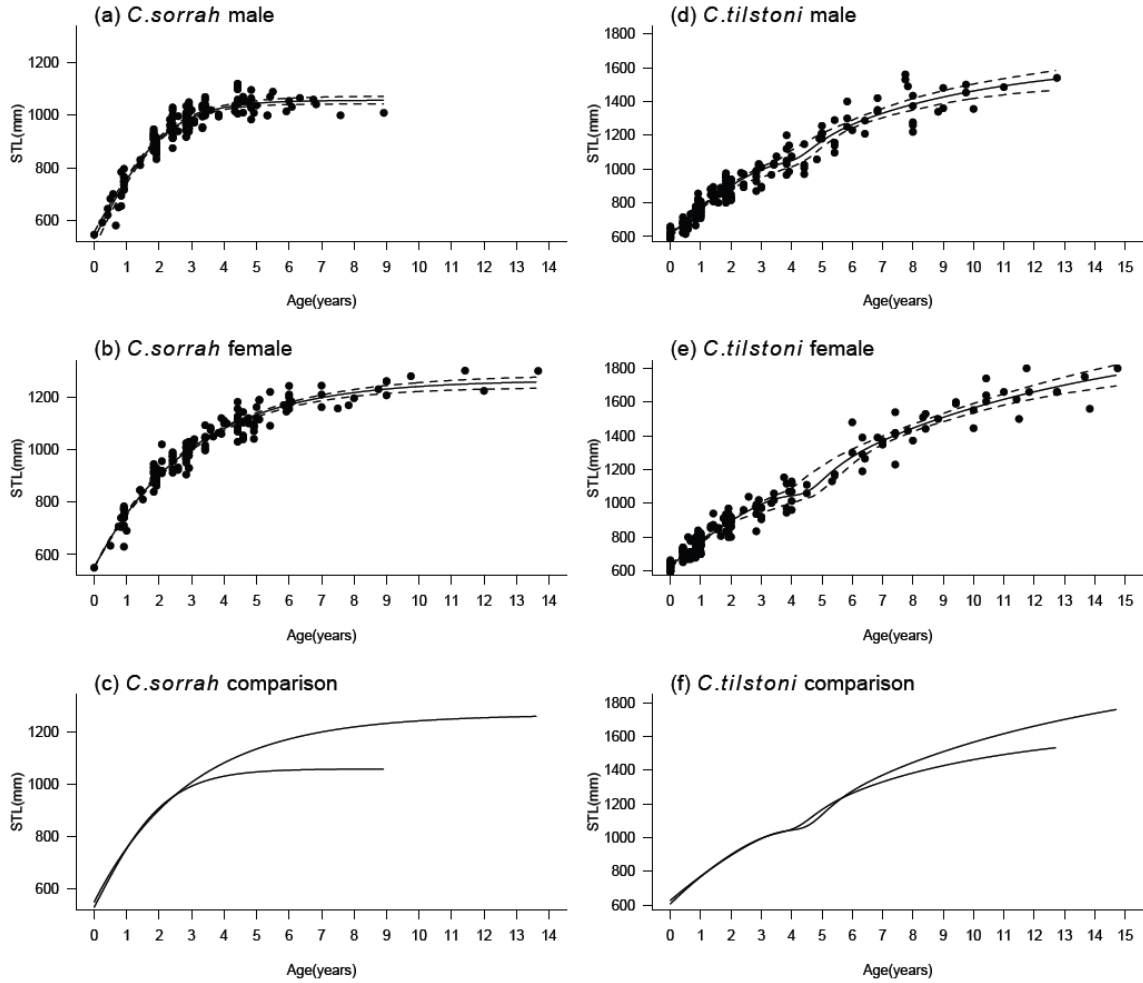


Figure 6.3 Length-at-age of *Carcharhinus sorrah* (a – c) and *C. tilstoni* (d – f) determined from vertebral growth analysis. Plots are mean STL at age (—) with 95% confidence intervals (---) and raw data (●), where mean values were computed using the preferred growth model selected from a candidate set of six based on AIC values.

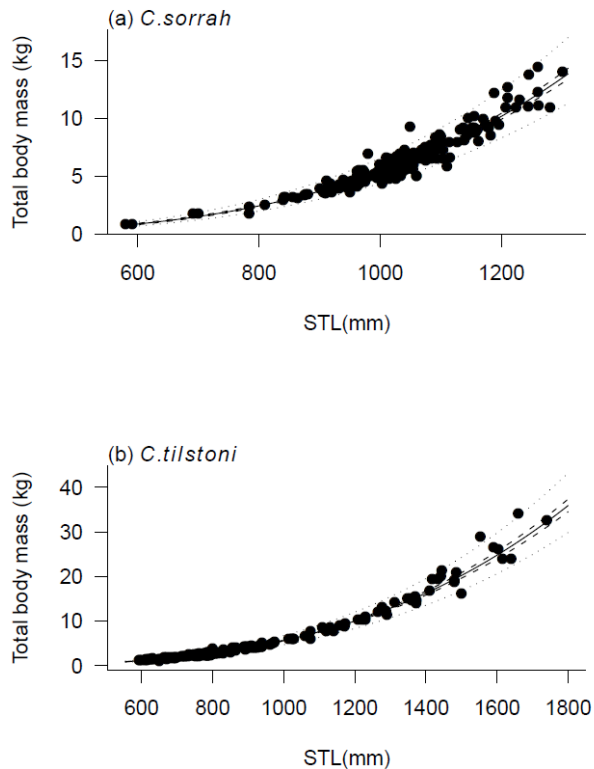


Figure 6.4 Relationships between total body mass and stretched total length of sharks. Plots are mean total body mass against STL (—), with 95% confidence intervals (---), 95% prediction intervals (----) and raw data (●) for (a) *Carcharhinus sorrah* and (b) *C. tilstoni*. Values of parameters and statistical quantities from linear regression analysis to derive the equation $W(l) = \beta_1 l^{\beta_2}$ are given in the following tabulation:

Species	β_1 (s.e. range) $\times 10^{-10}$	β_2 (s.e.)	n	r^2	rmse	P
<i>C. sorrah</i>	1.672 (1.087 - 2.571)	3.503 (0.430)	189	0.944	0.102	***
<i>C. tilstoni</i>	19.88 (16.59 - 23.82)	3.150 (0.027)	176	0.988	0.092	***

where W is body mass, l is STL, β_1 and β_2 are parameters, n is the number of individuals, r^2 is square of correlation coefficient and rmse is root mean square error for the regression $\log_e(W(l)) = \log_e(\beta_1) + \beta_2 l$. *P < 0.05, **P < 0.01, ***P < 0.001.

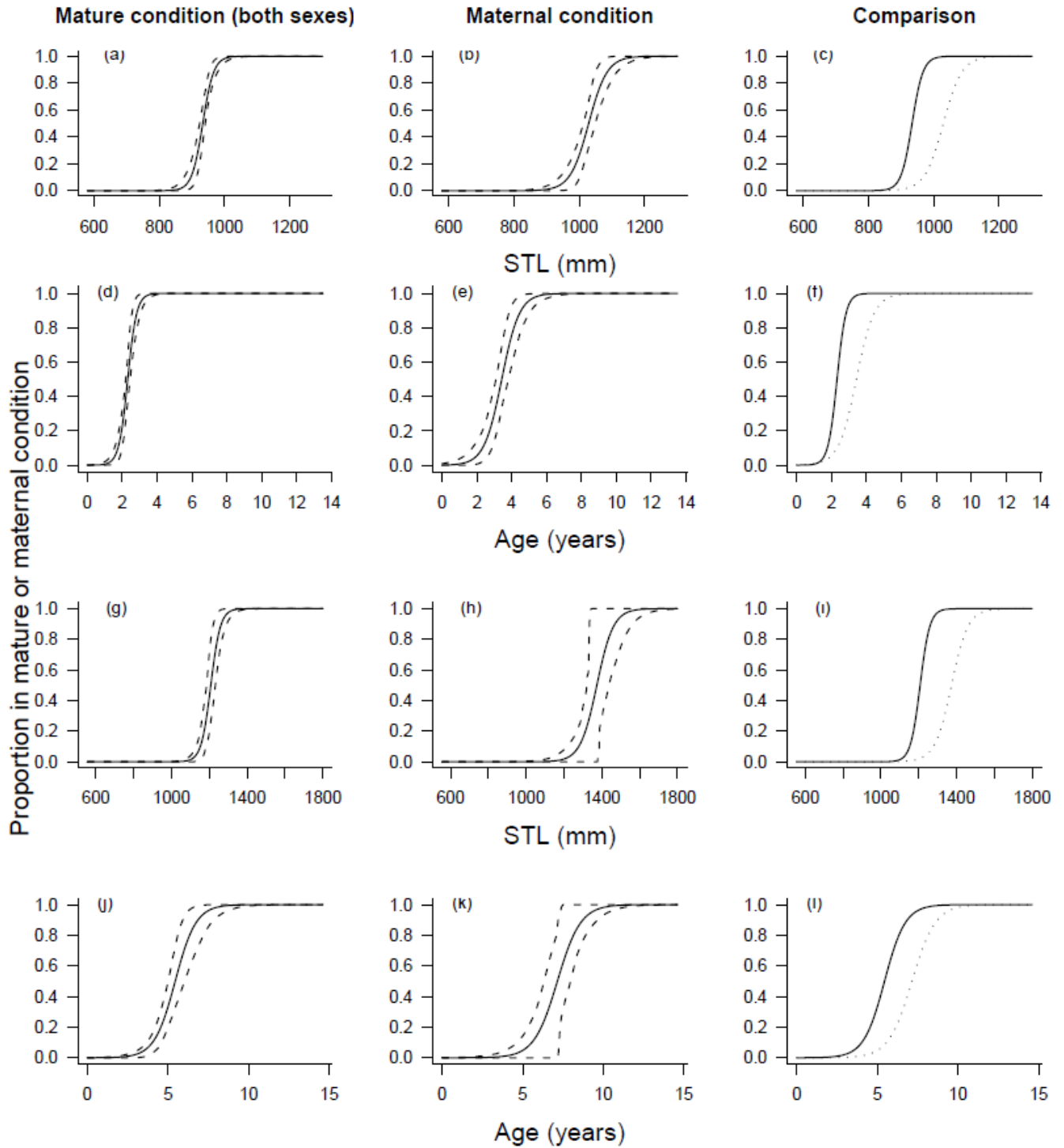


Figure 6.5 Length- and age-at-maturity and -maternity for *Carcharhinus sorrah* (a – f) and *C. tilstoni* (g – l). Proportion of both sexes mature or females in maternal condition against STL (—), with 95% confidence intervals (---). Values of parameters and statistical quantities for the equations $P(l) = (1 + \exp(-\ln(19)((l - \beta_1)/(\beta_2 - \beta_1)))^{-1}$ and $P(a) = (1 + \exp(-\ln(19)((a - \beta_1)/(\beta_2 - \beta_1)))^{-1}$ are given in the following tabulation:

Species	Figure	Analysis	β_1 (CI)	β_2 (CI)	n	N	ML	P
<i>C. sorrah</i>	a	Length-at-maturity	933.4 (924.4, 941.6)	982.7 (968.2, 1010)	340	427	-49.847	***
	b	Length-at-maternity	1029 (1011, 1047)	1112 (1077, 1170)	78	117	-25.689	***
	d	Age-at-maturity	2.345 (2.218, 2.502)	3.071 (2.767, 3.488)	153	209	-34.775	***
	e	Age-at-maternity	3.354 (2.885, 3.767)	5.068 (4.400, 6.080)	57	85	-23.802	***
<i>C. tilstoni</i>	g	Length-at-maturity	1208 (1187, 1233)	1282 (1244, 1330)	75	292	-15.959	***
	h	Length-at-maternity	1374 (1330, 1438)	1502 (1362, 1688)	24	108	-7.085	***
	j	Age-at-maturity	5.491 (5.029, 6.131)	7.382 (6.385, 8.905)	54	257	-25.371	***
	k	Age-at-maternity	7.446 (6.740, 8.375)	9.294 (7.734, 11.186)	23	107	-8.481	***

where l is STL (mm) and a is age (years), and P is the proportion of both sexes mature or females maternal at STL or age, β_1 and β_2 are parameters corresponding to l_{50} and l_{95} or a_{50} and a_{95} respectively, n is the number of both sexes mature or females in maternal condition, N is the total number of individuals examined, ML is maximum likelihood and P is the probability of statistical significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

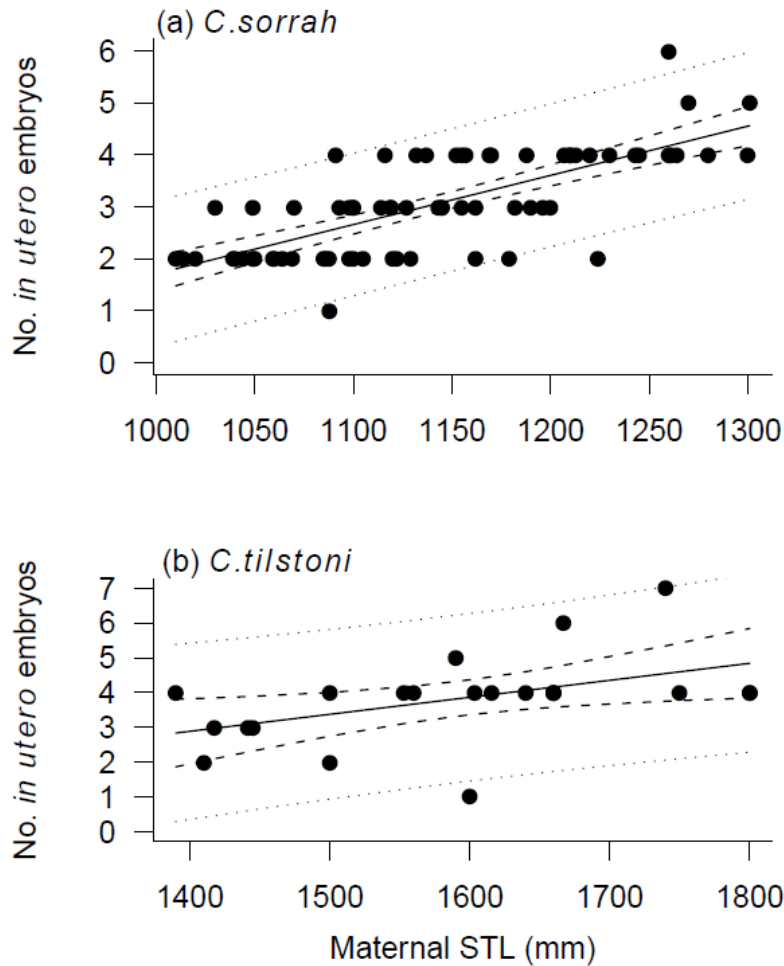


Figure 6.6 Number of *in utero* embryos against maternal STL. Plots are mean number of embryos against STL (—), with 95% confidence intervals (---), 95% prediction intervals (----) and raw data (●) for (a) *Carcharhinus sorrah* and (b) *C. tilstoni*. Values of parameters and statistical quantities for the linear regression $F(l) = \beta_1 + \beta_2 l$ are given in the following tabulation:

Species	β_1 (s.e. range)	β_2 (s.e.) x 10^{-3}	n	r^2	rmse	<i>P</i>
<i>C. sorrah</i>	-7.751 (-8.986 – -6.515)	9.463 (8.383 – 10.54)	71	0.520	0.682	***
<i>C. tilstoni</i>	-3.691 (-7.128 – -0.7937)	4.889 (2.904 – 6.874)	22	0.194	1.130	*

where l is STL (mm), and F is fecundity, β_1 and β_2 are parameters, n is the number of individuals, r^2 is square of correlation coefficient and rmse is root mean square error and P is the probability of statistical significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

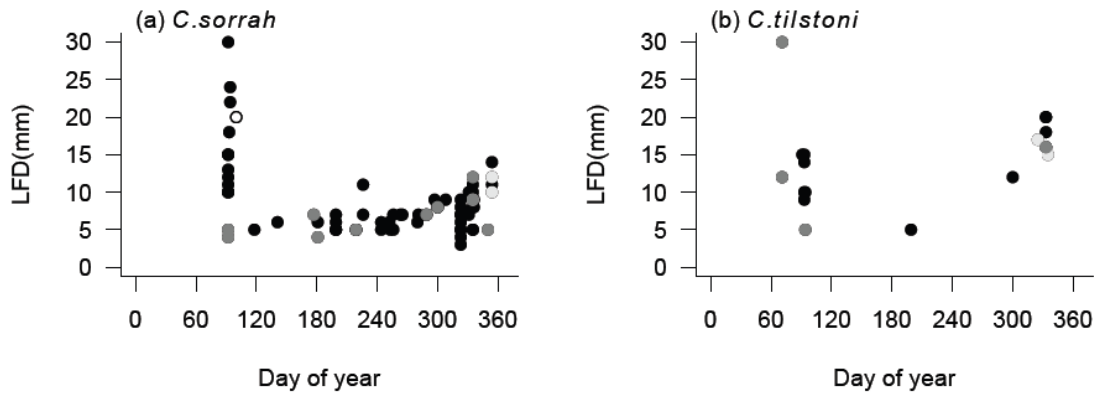


Figure 6.7 Largest follicle diameter (LFD) against day of year for (a) *Carcharhinus sorrah* and (b) *C. tilstoni*. Plots are raw data for each of the four adult female uterus stages: U = 3 (●); U = 4 (○); U = 5 (●); and U = 6 (●).

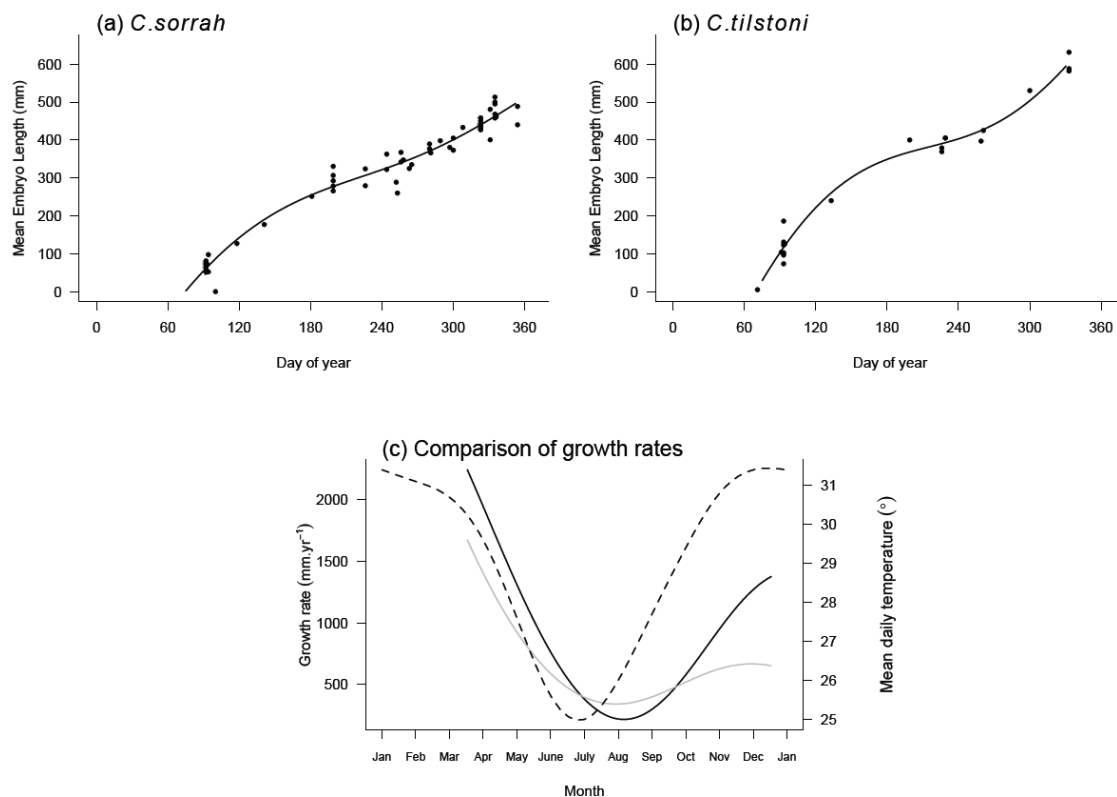


Figure 6.8 Mean embryo length against day of year for (a) *Carcharhinus sorrah* and (b) *C. tilstoni*, and (c) a comparison of mean embryonic growth rate and mean daily temperature against month. Plots (a) and (b) are mean embryonic STL at age (—) and raw data (●). Plot (c) is mean embryonic growth rate throughout the gestation period for *C. sorrah* (—) and *C. tilstoni* (---) and mean daily temperature (·····). Values of parameters and statistical quantities for the non-linear regression

$L(t) = \beta_1 - \beta_1 e^X$, $X = -\beta_2(t - \beta_3) - \frac{\beta_2\beta_4}{2\pi} \sin 2\pi(t - \beta_5) + \frac{\beta_2\beta_4}{2\pi} \sin 2\pi(\beta_3 - \beta_5)$ used in plots (a) and (b) are given in the following tabulation:

Species	β_1	β_2	β_3	β_4	β_5	n	rse
<i>C. sorrah</i>	1108	0.9000	-0.0013	0.4686	-0.1062	63	26.860
<i>C. tilstoni</i>	2553	0.4905	-0.0151	0.7261	2.8835	21	28.370

where L is STL in mm, t is time in years, β_1 is asymptotic length (L_∞) in mm, β_2 is the Brody growth coefficient K in years⁻¹, β_3 is t_0 in years, β_4 is the magnitude of oscillations in growth, and β_5 is the time at which zero growth begins.

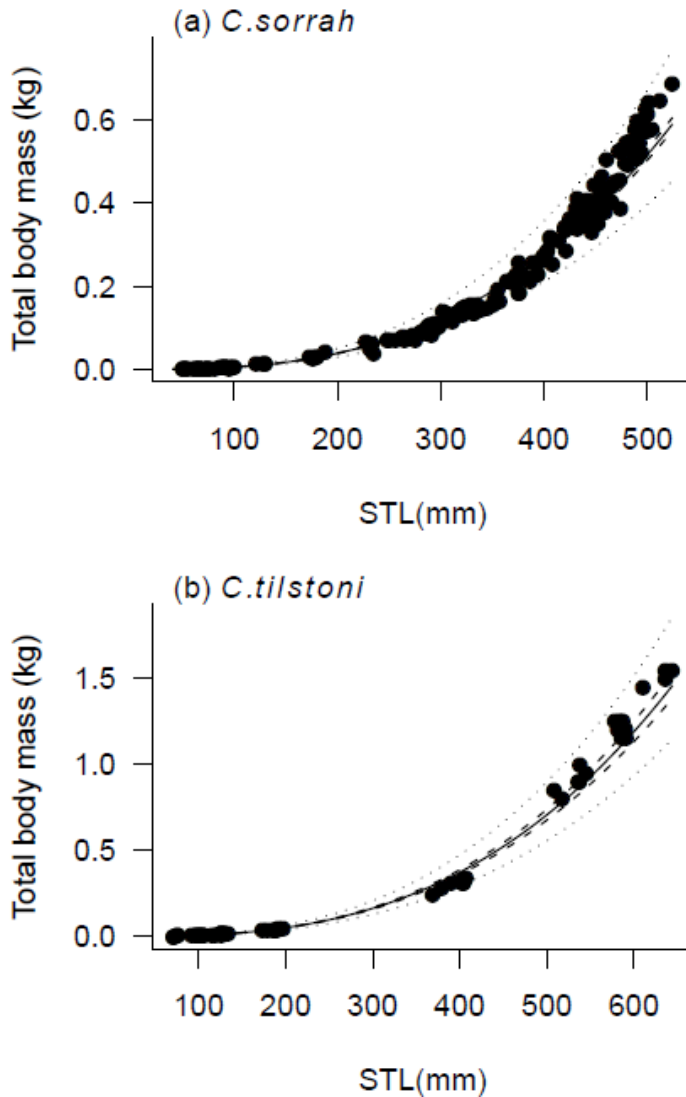


Figure 6.9 Relationships between *in utero* total body mass and stretched total length of embryonic sharks. Plots are mean total body mass against STL (—), with 95% confidence intervals (---), 95% prediction intervals (----) and raw data (●) for (a) *Carcharhinus sorrah* and (b) *C. tilstoni*. Values of parameters and statistical quantities from linear regression analysis to derive the equation $W(l) = \beta_1 l^{\beta_2}$ are given in the following tabulation:

Species	β_1 (s.e. range) $\times 10^{-8}$	β_2 (s.e.)	n	r^2	rmse	P
<i>C. sorrah</i>	1.217 (1.120 - 1.322)	2.826 (0.0147)	189	0.995	0.133	***
<i>C. tilstoni</i>	1.381 (1.235 - 1.543)	2.857 (0.020)	59	0.997	0.118	***

where W is body mass, l is STL, β_1 and β_2 are parameters, n is the number of individuals, r^2 is square of correlation coefficient and rmse is root mean square error for the regression $\log_e(W(l)) = \log_e(\beta_1) + \beta_2 l$. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

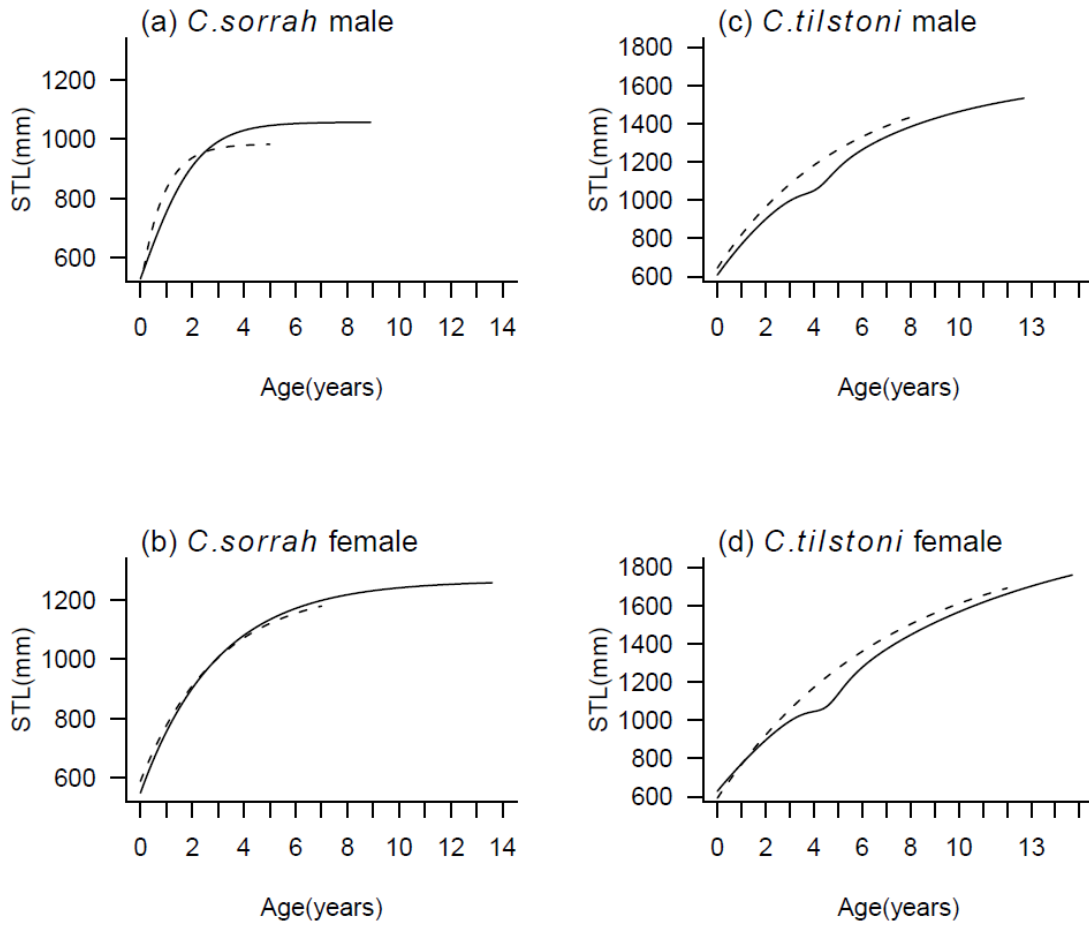


Figure 6.10 A comparison of growth curves derived from vertebral ageing of *Carcharhinus sorrah* and *C. tilstoni* from the GBRWHA (—) in the present study and from the Arafura Sea (---) by Davenport and Stevens (1988).

Table 6.1 Set of candidate models chosen for analysis of growth where length, L , is a function of time, t . Parameter β_1 , common to all models, is asymptotic length (L_∞) in mm and L_0 is length at birth in mm. All other parameters are not directly comparable.

Model	Potential process and parameter description	Growth function
Three parameter von Bertalanffy (VB3)	Growth rate decreases linearly with increasing length: β_1 is L_∞ (mm), β_2 is L_0 (mm), β_3 is k (years ⁻¹), the relative growth rate.	$L(t) = \beta_2 + (\beta_1 - \beta_2)(1 - \exp(-\beta_3 t))$
Two parameter von Bertalanffy (VB2)	Growth rate decreases linearly with increasing length, known L_0 is incorporated: β_1 is L_∞ (mm) and β_2 is k (years ⁻¹), the relative growth rate.	$L(t) = L_0 + (\beta_1 - L_0)(1 - \exp(-\beta_2 t))$
Two phase von Bertalanffy (TPVB)	Growth occurs in two distinct phases, during each phase growth rate decreases linearly with increasing length: β_1 is L_∞ (mm), β_2 is t_0 (year), β_3 is k (years ⁻¹), the relative growth rate, β_4 is that age (years) at which the transition between the two growth phases occurs, and β_5 is the magnitude of maximum difference between the two phases of growth.	$L(t) = \beta_1(1 - \exp(-\beta_3 A_t(t - \beta_2))),$ $A_t = 1 - \beta_4((t - \beta_5)^2 + 1)$
Three parameter Gompertz (GOM3)	Growth rate decreases exponentially with increasing length: β_1 is L_∞ (mm), β_2 is L_0 (mm), β_3 is k (years ⁻¹), the relative growth rate.	$L(t) = \beta_1(\exp(-\beta_2 \exp(-\beta_3 t)))$
Two parameter Gompertz (GOM2)	Growth rate decreases exponentially with length, known length at birth incorporated: β_1 is L_∞ (mm) and β_2 is k (years ⁻¹), the relative growth rate.	$L(t) = L_0 \exp(\log_e(\beta_1/L_0)(1 - \exp(-\beta_2 t)))$
Logistic	There is a sigmoidal relationship between growth rate and length: β_1 is L_∞ (mm), β_2 is the point of inflection (mm), β_3 (years ⁻¹), is the relative growth rate.	$L(t) = \frac{\beta_1 \beta_2 \exp(\beta_3 t)}{\beta_1 + \beta_2(\exp(\beta_3 t) - 1)}$

Table 6.2 Indices used for staging reproductive condition, adapted from Walker (2005)
Criteria for classing mature and immature condition

Organ	Index	Description	Maturity Assumption
Female			
Uterus	U=1	Uniformly thin tubular structure	Immature
	U=2	Thin, tubular structure, partly enlarged posteriorly	Immature
	U=3	Uniformly enlarged tubular structure	Mature
	U=4	<i>In utero</i> eggs present without macroscopically visible embryos present	Mature
	U=5	<i>In utero</i> embryos macroscopically visible	Mature
	U=6	Enlarged tubular structure distended	Mature
Male			
Clasper	C=1	Pliable with no calcification	Immature
	C=2	Partly calcified	Immature
	C=3	Rigid and fully calcified	Mature

Table 6.3 Recapture details of six calcein marked *Carcharhinus sorrah*

	Date release	STL _{Release} (mm)	Date recaptured	STL _{Recap} (mm)	Days at liberty	Growth (mm)	Bands pairs formed	Sex
1	14/05/2008	1260	18/11/2008	1245	188	-15	No mark	Female
2	18/04/2008	1240	26/11/2008	1224	222	-16	No mark	Female
3	27/05/2008	1160	21/05/2009	1157	359	-3	Unclear	Female
4	28/10/2008	1050	26/06/2009	1054	241	4	1	Female
5	4/04/2008	1110	30/06/2009	1039	452	-71	No mark	Female
6	9/09/2009	1240	22/09/2010	1264	378	24	No mark	Female

Table 6.4 Comparison of six growth models fitted to length-at-age data for two species of carcharhinid shark. The best model (in bold) was the one with the lowest value for Akaike's Information Criteria (AIC). The relative support of other models can be gauged based on Akaike differences (Δ), Akaike weights (w) and residual standard error (R.S.E.). K is the number of estimated parameters, +1 for variance. Best-fit estimates are given for parameters β_1 - β_5 (with 95% CI) as described in Table 6.1.

Sex	Model	n	K	AIC	Δ	w (%)	R.S.E.	β_1	β_2	β_3	β_4	β_5
<i>C. sorrah</i>												
M	VB3	151	3	1523	7.49	1.64	36.85	1072 (1056, 1092)	487.7 (430.6, 522.7)	0.6419 (0.5694, 0.7292)		
	VB2	151	2	1533	17.30	0.01	38.19	1085 (1067, 1107)	0.5513 (0.5005, 0.6040)			
	TPVB	151	5	1522	6.22	3.09	36.46	1065 (1050, 1091)	-1.180 (-2.014, -0.687)	0.6491 (0.4967, 0.8084)	0.1491 (-0.2043, 0.2669)	0.7721 (0.0733, 2.171)
	GOM3	151	3	1517	2.21	23.06	36.21	1063 (1049, 1080)	511.0 (466.9, 537.6)			
	GOM2	151	2	1522	6.48	2.72	36.85	1072 (1057, 1088)	0.6948 (0.6479, 0.7467)			
	Logistic	151	3	1515	0.00	69.48	35.95	1057 (1044, 1072)	530.3 (493.4, 554.2)	0.9027 (0.8209, 0.9972)		
F	VB3	143	3	1444	1.44	21.31	37.18	1271 (1241, 1299)	561.9 (529.7, 590.2)	0.3268 (0.2909, 0.3679)		
	VB2	143	2	1443	0.00	43.74	37.12	1265 (1240, 1288)	0.3389 (0.3162, 0.3635)			
	TPVB	143	5	1444	0.50	34.08	36.81	1309 (1258, 1365)	-3.260 (-5.290, -1.915)	0.2412 (0.171, 0.325)	0.3100 (0.0719, 0.6420)	0.01566 (-0.9791, 0.7027)
	GOM3	143	3	1451	7.97	0.81	38.04	1253 (1223, 1281)	591.4 (562.4, 620.3)			
	GOM2	143	2	1458	14.34	0.03	39.03	1231 (1208, 1254)	0.4674 (0.4384, 0.4988)			
	Logistic	143	3	1459	15.78	0.02	39.09	1240 (1211, 1270)	613.4 (583.8, 642.2)	0.488 (0.4270, 0.5534)		
<i>C. tilstoni</i>												
M	VB3	203	3	2214	8.04	1.68	55.87	1761 (1631, 1972)	622.0 (610.4, 633.6)	0.1336 (0.1048, 0.1604)		
	VB2	203	2	2213	6.16	4.29	55.75	1748 (1631, 1910)	0.1368 (0.1148, 0.1590)			
	TPVB	203	5	2206	0.00	93.39	54.51	1652 (1558, 1813)	-2.702 (-3.188, -2.427)	0.1712 (0.1335, 0.1997)	0.123 (-0.0157, 0.1858)	4.149 (3.024, 4.661)
	GOM3	203	3	2217	10.92	0.40	56.27	1612 (1517, 1724)	633.4 (622.2, 645.7)			
	GOM2	203	2	2219	12.15	0.21	56.58	1573 (1495, 1657)	0.2406 (0.2182, 0.2661)			
	Logistic	203	3	2222	15.82	0.03	56.95	1541 (1459, 1625)	643.4 (632.4, 655.9)	0.3085 (0.2751, 0.3461)		
F	VB3	226	3	2442	14.29	0.08	53.11	2280 (2016, 2641)	637.2 (627.3, 646.8)	0.08172 (0.0623, 0.1055)		
	VB2	226	2	2448	20.67	0.00	53.99	2138 (1959, 2334)	0.09587 (0.0809, 0.1143)			
	TPVB	226	5	2428	0.00	99.83	51.24	2046 (1868, 2296)	-3.399 (-3.929, -2.973)	0.1087 (0.0834, 0.1367)	0.1397 (0.0714, 0.2019)	4.509 (3.208, 5.080)
	GOM3	226	3	2442	14.31	0.08	53.12	1946 (1816, 2091)	647.7 (638.2, 657.0)			
	GOM2	226	2	2464	36.18	0.00	55.87	1843 (1752, 1936)	0.1894 (0.1721, 0.2086)			
	Logistic	226	3	2446	18.75	0.01	53.64	1818 (1722, 1914)	656.8 (647.6, 666.3)	0.2419 (0.2184, 0.2684)		

Table 6.5 Length-at-maturity and length-at-maternity sample sizes for *Carcharhinus sorrah*. A male was classed in mature condition if the clasper was rigid and fully calcified (C=3); otherwise it was classed as immature. A female was classed in mature condition if the uterus was uniformly enlarged and tubular in structure (U ≥ 3); otherwise it was class as non-mature. A female was classed as in maternal condition if U ≥ 4 or U > 3 if the largest ovarian follicle diameter was >10 mm between January and March; otherwise it was classed as in non-maternal condition.

Length class (mm) / age class (years)	Clasper condition			Mature Condition			Uterus condition						Mature condition			Maternal Condition			
	1	2	3	No	Yes	Total	1	2	3	4	5	6	No	Yes	Total	No	Yes	Total	
<600	2			2		2													
600-699	6			6		6	2						2		2	2			2
700-799	12			12		12	5						5		5	5			5
800-899	23	1		24		24	5						5		5	5			5
900-999	12	9	74	21	74	95	6	3	8				9	8	17	17			17
1000-1099			159		159	159			8	1	23			32	32	8	24		32
1100-1199	1		11	1	11	12			2		31	3		36	36	2	34		36
1200-1299											18			18	18		18		18
≥ 1300											2			2	2		2		2
Total	56	10	244	66	244	310	18	3	18	1	74	3	21	96	117	39	78		99
< 1	16			16		16	6						6		6	6			6
1-1.99	15	1		16		16	5						5		5	5			5
2-2.99	2	6	28	8	28	36	2	1	6		1		3	7	1	9	1		1
3-3.99	1		17	1	17	18	1		3		7	1	1	11	12	4	8		12
4-4.99			26		26	26			4	1	19			24	24	4	2		24
5-5.99			6		6	6					1			1	1		1		1
6-6.99			3		3	3					5	1		6	6		6		6
7-7.99			2		2	2					3	1		4	4		4		4
8-8.99			1		1	1					4			4	4		4		4
9-9.99											1			1	1		1		1
10-10.99																			
11-11.99											2			2	2		2		2
12-12.99																			
≥ 13											1			1	1		1		1
Total	34	7	83	41	83	124	14	1	13	1	53	3	15	7	85	28	57		84

Table 6.6 Length-at-maturity and length-at-maternity sample sizes for *Carcharhinus tilstoni*. A male was classed in mature condition if the clasper was rigid and fully calcified (C=3); otherwise it was classed as immature. A female was classed in mature condition if the uterus was uniformly enlarged and tubular in structure ($U \geq 3$); otherwise it was class as non-mature. A female was classed as in maternal condition if $U \geq 4$ or $U > 3$ if the largest ovarian follicle diameter was >10 mm between January and March; otherwise it was classed as in non-maternal condition.

Length class (mm) / age class (years)	Clasper condition			Mature Condition			Uterus condition						Mature condition			Maternal Condition		
	1	2	3	No	Yes	Total	1	2	3	4	5	6	No	Yes	Total	No	Yes	Total
<600	2			2		2	2						2		2	2		2
600-699	22			22		22	11						11		11	11		11
700-799	39			39		39	23						23		23	23		23
800-899	31			31		31	19	1					20		20	20		20
900-999	19			19		19	14						14		14	14		14
1000-1099	9	3		12		12	3						3		3	3		3
1100-1199	6	3	2	9	2	11	2	3					5		5	5		5
1200-1299	1	3	14	4	14	18		1	2				1	2	3	3		3
1300-1399			12		12	12			3				4		4	2	2	4
1400-1499			13		13	13							4	1	5		5	5
1500-1599			5		5	5			1				5		6	1	5	6
1600-1699													8		8		8	8
1700-1799													2		2		2	2
≥ 1800													2		2		2	2
Total	129	9	46	138	46	184	74	5	6		21	2	79	29	108	85	23	108
< 1	59			59			36						36		36	36		36
1-1.99	34			34			26	1					27		27	27		27
2-2.99	12	2		14			6						6		6	6		6
3-3.99	6	2		8			4						4		4	4		4
4-4.99	4	1	6	5	6		2						2		2	2		2
5-5.99	2	1	4	3	4			2				1	2	1	3	2	1	3
6-6.99			3	3	3			1	5				1	5	6	5	1	6
7-7.99		1	6	1	6			1				2	1	1	4	1	3	4
8-8.99			2	2	2				1			2		3	3	1	2	3
9-9.99			3	3	3							4		4	4		4	4
10-10.99			1	1	1							4		4	4		4	4
11-11.99												3		3	3		3	3
12-12.99			1	1	1							2		2	2		2	2
13-13.99												2		2	2		2	2
≥ 14												1		1	1		1	1
Total	117	7	26	124	26		74	5	6		2	2	79	28	17	85	22	17

Table 6.7 Hypothesis testing for the effect of sex on length- and age-at-maturity. Analysis of deviance tables testing for a significant effect of sex and its interaction on STL and age.

Species	Source of variation	Length-at-maturity			Age-at-maturity		
		d.f.	χ^2	<i>P</i>	<i>df.</i>	χ^2	<i>P</i>
<i>C. sorrah</i>	STL/Age	1	332.05	<0.001***	1	173.932	<0.001***
	Sex	1	2.71	0.0995	1	0.363	0.547
	STL/Age x Sex	1	3.03	0.0816	1	0.372	0.542
	Residual	426			208		
<i>C. tilstoni</i>	STL/Age	1	300.81	<0.001***	1	215.382	<0.001***
	Sex	1	2.43	0.1192	1	2.941	0.0863
	STL/Age x Sex	1	2.49	0.1145	1	0.105	0.746
	Residual	291			256		

Chapter 7. Evaluating the perils and possibilities associated with sex-biased harvesting of widely distributed sharks



Plate 7. Adult male scalloped hammerhead, *Sphyrna lewini*, caught in Halifax Bay (April 2009).

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7.1 INTRODUCTION

The demand for protein to feed the world's growing population has led to expansion of industrialised commercial fisheries into all but the most inaccessible of aquatic habitats (Morato *et al.*, 2006). Top-down fishing of these ecosystems has since resulted in the rapid loss of large predatory fish from many of the world's oceans (Pauly *et al.*, 1998; Christensen *et al.*, 2003; Myers and Worm, 2003; Myers *et al.*, 2007). Although elasmobranchs (shark and rays) have not traditionally been the focus of such fisheries, when they have been targeted or caught as by-catch their populations have often shown low resilience to fishing (Walker, 1998; Stevens *et al.*, 2000a; Dulvy *et al.*, 2008). A further pressure on sharks in recent decades has been the industrialisation of China where the demand for shark fin soup from a burgeoning middle class has inflated the price of shark fins causing a surge in demand worldwide (Clarke *et al.*, 2007).

The susceptibility of sharks to overexploitation is due partly to their large body sizes, a feature often implicitly tied to life history traits like late-maturation, slow-growth and high-longevity (Charnov and Berrigan, 1990; Beverton, 1992; Froese and Binohlan, 2000). Compounding this are the reproductive strategies of sharks, which involve internal fertilisation and are more similar to those of mammals and birds than other fish (Wourms, 1977). Consequently, sharks often have fecundities several orders of magnitude lower than many broadcast spawning teleosts (Goodwin *et al.*, 2002). As such, recruitment is closely tied to adult-biomass, and there is thought to be lower capacity for density dependent compensation in population growth rate after depletion has occurred (Sminkey and Musick, 1995; Taylor and Gallucci, 2009).

Currently management and conservation of sharks is impeded by a poor knowledge of their behaviour — a systemic issue in aquatic conservation (Shumway, 1999). An ignorance of animal behaviour can result in ineffective management strategies. For example, UK protection zones were shown to be of limited use for the migratory basking shark, *Cetorhinus maximus* (Gunnerus 1765) as tagged individuals spent 78% of their time outside of protected areas (Southall *et al.*, 2006). In addition to their often complex migration patterns and habitat preferences, most shark populations also segregate by size and sex (Springer, 1967; Sims, 2005). In large and wide-ranging species e.g. blue shark, *Prionace glauca* (Linnaeus 1758), these segregation and migration patterns may manifest themselves at the scale of entire oceans, with males, females and juveniles occupying entirely different habitats and locations (Stevens, 1990; 1992; Litvinov, 2006). For

wide-ranging sharks an appreciation and understanding of these types of behaviours is therefore needed for effective conservation and management.

The propensity of sharks to segregate by sex is one particular aspect of their behaviour that may have profound implications for fishery exploitation, especially if it results in the differential harvest of certain components of the population. The phenomenon of sex segregation is common among vertebrates (Ruckstuhl and Neuhaus, 2005) and is ubiquitous among shark populations at some scale (Sims, 2005). Despite its prevalence, there has been little investigation into the possible effects that differential harvest has on population dynamics. Indeed, where sex-biased harvest has occurred in terrestrial animals such as ungulates and ursids, there have often been unexpected negative outcomes (McLoughlin *et al.*, 2005; Milner *et al.*, 2007). Given the conservative life histories of many large sharks, it is thought that sex-biased harvest may exacerbate the effects of commercial fishing (Mucientes *et al.*, 2009). Contrasting this however, male-biased harvest has been suggested as an explanation for the apparent resilience of some shark populations to high levels of fishing (Simpfendorfer *et al.*, 2002a). Furthermore, because the sex of sharks can easily be determined externally, the selective harvest of males has also been suggested as a potential management strategy to reduce mortality on females (Camhi *et al.*, 1998; Walker, 2005a).

We investigated the implications of sex-biased harvesting for conservation and management of wide-ranging large sharks using the scalloped hammerhead, *Sphyrna lewini*, as a case study. Sex segregation is a well-documented feature of *S. lewini* populations with females migrating offshore at smaller sizes than males to exploit higher energy pelagic prey (Klimley, 1987; Stevens and Lyle, 1989). This formerly abundant large shark is fished throughout its range and is presently regarded by the IUCN as globally Endangered (Baum *et al.*, 2007). To simulate the effects of sex-biased harvesting on population dynamics we conducted a demographic analysis using stochastic, age-structured, matrix models (Caswell, 2001; Cortés, 2002). Demographic analyses using matrix models and life tables have become popular in recent years for modelling population dynamics in elasmobranchs and other data-limited taxa (Heppell *et al.*, 2000; Cortés, 2007) and can often provide useful insights into how perturbations in life history parameters (especially survival) can affect population growth rates.

We simulated the effect of sex-biased harvesting on the population dynamics of *S. lewini* by incorporating catch data from three fisheries harvesting this species in the Indo-Australia region.

‘Fishery A’ was a coastal gillnet fishery operating in tropical northern Australia. Catch of *S. lewini* by this fishery was strongly biased towards males and young juveniles of both sexes (Chapter 2). ‘Fishery B’ was a mid-shelf (30–100 m depth), demersal longline fishery operating off the east coast of Australia in sub-tropical waters. Although the overall sex-ratio of this fishery was approximately equal, mature females were a minor component of the catch that included mainly adult males and immature females (Macbeth *et al.*, 2009). Finally, ‘Fishery C’ was a pelagic longline fishery operating in Indonesian waters (White *et al.*, 2008) and encountered primarily females. For each fishery scenario we quantify and compare the effects of sex-biased harvesting on population dynamics of *S. lewini*. In doing so we examine the merits of this concept as a potential tool for conservation or increasing sustainable yield in fisheries catching wide-ranging sharks (Brander, 2010). We also discuss the potentially negative effects that might result from demographic manipulation of a population, particularly in relation to the reproductive strategy used by elasmobranch fishes.

7.2 METHODS

7.2.1 Conceptual model of sex segregation in *S. lewini*

The life cycle of *S. lewini* is typical of many large coastal-pelagic sharks in that it involves a depth-ward migration with increasing size and age. Neonate *S. lewini* are born in shallow coastal areas where they spend the early part of their lives (Clarke, 1971). However, habitat preferences of males and females appear to diverge at an early age with females dispersing from their natal areas at smaller sizes than males (Klimley, 1987). In addition to this, reproductively mature males are often recorded in coastal areas, suggesting that some males may never disperse from their coastal nurseries (Chapter 4). These factors appear to contribute to the strongly male-biased sex ratio that is commonly observed in coastal waters and also the larger mean size of males in those areas compared to females (Branstetter, 1981; 1987b; Stevens and Lyle, 1989; Lessa *et al.*, 1998; Dudley and Simpfendorfer, 2006) (Chapter 2). The movements of adult females have been less well documented although evidence suggests that, with the exception of entering coastal waters to pup, females are almost exclusively pelagic or meso-pelagic (Klimley and Nelson, 1981; Chen *et al.*, 1990; Jorgensen *et al.*, 2009). Assuming that the sex ratio at birth is equal (Chen *et al.*, 1988; White *et al.*, 2008), then the higher proportion of males in coastal areas, combined with the preference for greater depths by females may contribute to the often heavily female-biased sex ratio of *S. lewini* observed in or near pelagic habitats (Klimley and Nelson, 1981; Chen *et al.*, 1988; White *et al.*, 2008).

It follows that the mean length of individuals occurring at a given depth depends on their preference for that depth, and their sex (Figure 7.1 a). The differing habitat preferences of females and males should also result in a sex-ratio gradient from male-biased in coastal waters to female biased in pelagic waters (Figure 7.1 a). This can be seen in the waters off eastern Australia, where length is a linear function of depth for both sexes in depths <25 m (Figure 7.1 b). For a fishery encountering *S. lewini*, age structure and sex-ratio of the population will be affected differently depending on what depth the fishery operates at.

7.2.2 Matrix population model

An age-structured, matrix population model was constructed following Caswell (2001). Life history information was initially organised into the form of a life-table, with vectors of survival, l_x , and fecundity, m_x (Stearns, 1992). Life tables were then re-arranged into a Leslie Matrix for statistical analysis (Caswell, 2001) where the projection matrix, A is given by

$$\mathbf{A} = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 & \dots & f_{x-1} \\ s_1 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{x-1} & 0 \end{bmatrix}$$

in which f and s are the age-specific values of fecundity and survival in a birth-pulse population with a pre-breeding census. The female population size, n , at time $t+1$, is given by

$$\mathbf{n}(t + 1) = \mathbf{A}_{n,t} \mathbf{n}(t).$$

The instantaneous rate of population growth, λ , is the dominant eigenvalue of the projection matrix, \mathbf{A} (Caswell, 2001) and population doubling time was calculated as

$$t_2 = \log_{\lambda} 2.$$

The rate at which the population increases from one generation to the next, R_0 , is the dominant eigenvalue of the matrix \mathbf{R} , which is calculated as the product of the fertility matrix \mathbf{F} , and the fundamental matrix, \mathbf{N} (Caswell, 2001). The generation time, T , the time it takes for the population to increase by a factor of R_0 , was calculated as

$$T = \frac{\log_e R_0}{\log_e \lambda}.$$

To further examine properties of the population, the reproductive value of individual age classes and stable age distribution (SAD) were obtained as the left and right eigenvectors of the projection matrix, \mathbf{A} . Elasticity analysis was carried out to examine how changes in survival

(summed across juvenile and adult age classes) and fertility (age-0 survival) were likely to affect λ .

7.2.3 Life history data

Published life history information necessary to create population models are available for *S. lewini* from many parts of the world including the east coast of Australia and Indonesia (White *et al.*, 2008) (Chapter 4). Like many large sharks however, it is often difficult to obtain accurate information for basic vital rates. For *S. lewini* this is exacerbated by its sexual segregation behaviour, which often means one sex or life stage is sampled predominantly (White *et al.*, 2008). Uncertainty in life history parameters was therefore incorporated into the analysis using the Monte Carlo simulation approach described by Cortés (2002). Probability mass functions (PMFs) for key life history parameters were generated using data collected from global studies of this species. For a given population model, life history parameters were randomly selected from the PMFs. This process was repeated 1000 times to capture the uncertainty in the data.

7.2.4 Age and growth

The age and growth of *S. lewini* has been investigated off the east coast of Australia (Chapter 4), however there is considerable uncertainty in the growth rate parameter, k , and asymptotic length, L_{∞} as relatively few large females were captured. Uncertainty in these parameters was accounted for by incorporating information from three previous studies of female *S. lewini* in the Pacific Ocean (Chen *et al.*, 1990; Tolentino and Mendoza, 2001; Tolentino *et al.*, 2008), and two previous studies in the Gulf of Mexico (Branstetter, 1987b; Piercy *et al.*, 2007). A triangular PMF was developed for both k and L_{∞} using the minimum, maximum and median values from the above studies (Table 7.1, Figure 7.2 a–b). Longevity, A_{MAX} of *S. lewini* is also confounded by a lack of large females in all but two growth studies, and a lack of age-validation. Some studies of *S. lewini* have suggested that growth bands are formed annually in this species (Branstetter, 1987b; Piercy *et al.*, 2007), while others have suggested they are formed biannually (Chen *et al.*, 1990; Tolentino and Mendoza, 2001; Tolentino *et al.*, 2008). Although this issue is not resolved, for the purposes of this study we assumed that growth band pairs were formed annually in *S. lewini*, as they are in two other hammerhead species (Parsons, 1993; Passerotti *et al.*, 2010) (Chapter 4). Where studies assumed bi-annual growth band deposition, values were converted to represent annual growth band deposition (e.g. female A_{MAX} of 14 in Chen *et al.* (1990) became

28). Values for A_{MAX} were sampled randomly from a uniform probability distribution with a minimum of 28 and maximum of 31 (Table 7.1, Figure 7.2 c).

7.2.5 Maturity

No studies have directly modelled female maturity stage as a function of age, so age-at-maturity was determined by substituting length-at-maturity, L_{MAT} information into growth curves. A year was then added to account for the length of the reproductive cycle. There is little published information available on female length-at-maturity from Australian waters. The smallest mature, pre-ovulatory, pregnant and spent females recorded by Stevens and Lyle (1989) were 2280 mm, 2290 mm, 2380 mm and 2560 mm. A single mature female of 2600 mm was recorded in Chapter 4. The smallest of 15 pregnant females recorded from the Queensland Shark Control Program (QSCP) was 2300 mm (Wayne Sumpton, Pers. Comm.). The largest immature individual recorded in Chapter 4 was 1982 mm. Based on this information, female maturity was assumed to occur around 2200 mm in the waters surrounding Australia. Elsewhere in its range, female *S. lewini* mature at sizes between 1800 mm and 2450 mm (Chen *et al.*, 1988; Devadoss, 1988; Hazin *et al.*, 2001; Tolentino and Mendoza, 2001; Tolentino *et al.*, 2008; White *et al.*, 2008). A triangular PMF was developed for L_{MAT} using the minimum, maximum and median values in the above studies (Table 7.1, Figure 7.2 d).

7.2.6 Fecundity and timing of reproduction

Fecundity was determined from fifteen pregnant females captured by the QSCP (Wayne Sumpton, Pers. Comm.)(Table 7.1, Figure 7.2 e) for which there was a significant positive correlation between litter size and maternal length. Elsewhere, the relationship between fecundity and female length has been described in studies conducted in Indonesia and Taiwan (Chen *et al.*, 1988; White *et al.*, 2008). A significant positive correlation can also be found in the data of de Bruyn *et al.* (2005) from South Africa if an outlying data-point is removed. In the waters off Queensland, the fecundity of *S. lewini* was less than Indonesia and Taiwan, but greater than South Africa (Figure 7.2 e). Although the periodicity of reproduction in *S. lewini* from Australian waters is unknown, elsewhere it reproduces annually and has synchronous reproduction (Chen *et al.*, 1988; White *et al.*, 2008). Although reproduction is at least partially asynchronous in Australian waters, it appears that the majority of young are born during summer (Chapter 4). Hence a birth-pulse population model was preferred over a birth-flow model.

7.2.7 Survival

Survival rates have only been determined in the wild for a few elasmobranch species (Gedamke *et al.*, 2007), so age specific survival, s , was estimated using empirical relationships of natural mortality, M . Survival was then calculated as $s = e^{-M}$. Following the approach of McAuley *et al.* (2007a) three age-independent methods and two age-dependent methods for estimating mortality were calculated (Pauly, 1980; Hoenig, 1983; Peterson and Wroblewski, 1984; Chen and Watanabe, 1989; Jensen, 1996). The life history parameters needed to calculate these were randomly drawn from the above PMFs and age specific survival was calculated by taking the mean of all methods above (Table 7.2, Figure 7.2 f).

7.2.8 Quantitative evaluation of sex-biased harvesting

The effect of sex-biased harvesting on the population dynamics of *S. lewini* was examined by incorporating harvest rates from three commercial fisheries operating in the Indo-Australia region (Table 7.3). The age-classes available to each fishery were determined by converting length-frequency data to age-frequency data using the von Bertalanffy growth function. The authors had access to raw-length-frequency data from Fishery A and Fishery B, while length-frequency data for Fishery C was read directly from Figure 2 in White *et al.* (2008). Fishery mortality was then applied at a constant rate over all vulnerable age classes by multiplying the projection matrix, A , with a harvest matrix (Gallucci *et al.*, 2006). In each scenario the level of fishing mortality that the population could withstand before negative population growth rates occurred (i.e. $\lambda < 1.0$) was then iteratively searched for. The effect of fishing was then compared among scenarios.

7.3 RESULTS

7.3.1 Survival

Mean natural mortality estimates based on the 7 empirical methods ranged from 0.08 yr^{-1} for the method of Pauly (1980) to 0.152 yr^{-1} for the Hoenig (1983) (combined) method (Table 7.2). For the two methods that provided age-specific values, mortality rates range from 0.477 yr^{-1} for age-0 individuals using the Chen and Watanabe (1989) method to 0.067 yr^{-1} for age-30 individuals using the Peterson and Wroblewski (1984) method. These estimates of mortality produced a mean first-year survivorship of 84% (range 81-87%) and mean survivorship in terminal year of life of 2% (range 1-4%).

7.3.2 Population model for *S. lewini*

For the unfished population of *S. lewini*, population growth rates, λ , were between 0.99 and 1.217 yr^{-1} , with a mean of 1.108 yr^{-1} (Figure 7.3 a). Population growth rates of this level gave a mean population doubling time, t_2 , of 7.71 years. The truncated left-hand tail of the t_2 distribution indicated that t_2 values <4 years were extremely unlikely, although depending on the combination of resampled parameters, t_2 values >10 years were still reasonably common (Figure 7.3 b). The values for net reproductive rate, R_0 , were more normally distributed than population doubling time (Figure 7.3 c) and indicated that under conditions of exponential growth a newborn female would be expected to produce an average of 6.97 female offspring during her lifetime. Based on this the average generation time was 19.05 years (Figure 7.3 d).

Age-specific reproductive values were highest between ages 18 and 23, and it was these age classes that were most valuable in terms of current and future offspring (Figure 7.3 e). The stable age distribution of the population was predominantly composed of neonate (age 0) and juvenile individuals, which, numerically, were 87% of the population on average. However, depending on the set of resampled parameters juveniles were between 70 and 95% of the population (Figure 7.3 f). Mean fertility elasticity was 5.5% while mean juvenile and adult survival elasticities were 44.1% and 50.4%, respectively (Figure 7.4). Depending on the set of parameters chosen, juvenile survival and adult survival interchangeably exhibited the greatest influence on λ , although on average the elasticity of λ to adult survival was the highest. Elasticity ratios indicated that a decrease in either juvenile or adult survival of 10% would have to be compensated for by an 80% or 90% increase in fertility or age-0 survival respectively.

7.3.3 Incorporating sex-biased harvest

The age-frequency distribution for Fishery A (Figure 7.5 a) was dominated by neonates of both sexes, although the fishery also regularly captured larger males up to age 11 (1930 mm). Females were still common in the fishery at age 1, although none older than 2 (~1100 mm) were captured indicating they had likely dispersed offshore by this time. Females between the age of 0 and 2 were therefore considered available to this fishery. Under this level of fishing mortality, on average 45.2% of age 0 to 2 year old females could be harvested before population growth rates fell below zero (Figure 7.6 a). In addition to this, the male to female sex ratio in Scenario A was

1.80:1, and heavily skewed toward males. As such, the probability of catching females was nearly double that of males.

In Fishery B (Figure 7.5 b), the demersal longline fishery, the sex ratio was not significantly different from parity, however there was segregation by size. Males at all ages > 4 (~1528 mm) appeared to be available to this fishery and most were sexually mature. Conversely, the females captured by this fishery, were, with one exception sexually immature. Females in Scenario B were therefore considered available between the ages of 4 and 9. In this fishery, the population was able to sustain harvest rates of up to 26.8% on average before λ dropped below zero (Figure 7.6 b).

Fishery C represented a pelagic longline fishery in Indonesia. In this fishery both males and females of nearly all age classes were captured except neonates and one year olds, so all females > 2 year old were considered available to this fishery. Although adults were still captured by this fishery, pre-reproductive age classes were the major component of the fishery. Applying fishing mortality across available age classes predicted that on average 10.6% of females could be harvested before the population growth rates fell below zero (Figure 7.6 c). This was close to the value of λ obtained for the population, which suggested that the population was capable of growing, on average, by around 10.8% annually. However, the male to female sex ratio in this fishery was 1:5 so the probability of encountering females was also much higher.

7.3.4 Comparing the effects of sex-biased harvesting

In Fishery A, where fishing was restricted to the first three female age classes, fishing mortality of 45.5% on the available females was necessary to maintain stationary population growth ($\lambda=1.0$). As the population was capable of growing by, on average 10.8% per year, this level is approximately four times the level of fishing mortality the population could sustain if harvesting occurred on all age classes. In Fishery B, the female age classes captured by the fishery could sustain fishing mortality of up to 26.4% on larger juveniles (4–9 years old); approximately double the rate that the overall population was capable of growing by. In Fishery C, where all but the first two female age classes were available to the fishery, the level of fishing mortality the population could sustain (10.6%) effectively matched λ . This is expected given the low Age-0 survival elasticities that indicated survival of this age-class has little impact on λ .

7.4 DISCUSSION

The results of this study suggest that when fishing is restricted to only a small number of young age classes, the population can sustain higher fishing mortality than if fishing is spread evenly across all age classes. Most demographic studies on elasmobranchs have suggested that population growth rates are likely to be most influenced by changes in juvenile survival, and as such advocate protection of juveniles (Cortés, 2002; Frisk *et al.*, 2005). Owing to the lower survival elasticities of older age classes, harvest of the adults should lead to the highest yield per recruit (Gallucci *et al.*, 2006). However, because the survival elasticities of individual age classes themselves are relatively small, when harvest is restricted exclusively to only a few age classes (including juveniles), then higher levels of fishing mortality can be sustained than if all age classes were harvested equally (Simpfendorfer, 1999). Because harvest of individuals in Fishery A and Fishery B was restricted to a few age classes, these fisheries were able to sustain higher levels of fishing mortality. However, these fisheries also have the advantage that males are captured at larger sizes than females, and, for Fishery A, are also captured more frequently. Hence in Fishery A and Fishery B, females are captured in a way that allows higher fishing mortality, while males are captured in a way that maximises yield.

7.4.1 Viability of sex-biased harvesting for managing sharks

Although the male-biased harvest in Fishery A and Fishery B off eastern Australia is not a management strategy, but rather occurring incidentally, demographic models suggest that this method could potentially be used to reduce the risk of overfishing of females. For such a strategy to be intentionally implemented, it would necessitate a detailed knowledge of the habitat preferences of the target species. The life cycles of large pelagic fish including sharks are likely to be highly complex, although from the limited information presented in Figure 7.1 b, it seems plausible that the measurement of even a single explanatory variable (e.g. depth) could provide enough information to devise a useful management strategy. Furthermore, while some shark species might be perceived as generalists in their habitat use e.g. *Galeocerdo cuvier* (Péron & Lesueur 1822), most appear to have strong affinities and preferences for particular habitats. In Fishery A, although neonate *S. lewini* were regularly captured (Chapter 2), no adult females were captured despite sampling regularly over four years. In a similar fishery operating in the Arafura Sea, Stevens & Lyle (1989) recorded only four pregnant females out of a total of 5580 *S. lewini* over six years. The habitat preference of *S. lewini* between sexes is so markedly different that

despite its abundance and cosmopolitan distribution, prior to 1988 only three pregnant females had been recorded in the primary literature (Clarke, 1971; Bass *et al.*, 1975). Observations such as this suggest that the habitat preferences of some species are spatially and temporally stable enough to be useful for designing sex-specific harvest strategies.

While it might be concluded that sex-biased harvest is a logistically viable way of balancing both harvest and conservation in large sharks, there is a major assumption that potentially undermines any benefits that could be derived from it. This study assumes that the population dynamics of *S. lewini* can be adequately represented by a female-only model, and that female fecundity limits the rate of population growth. This implies that male fertility is not a limiting factor in population growth. For other fish such as broadcast spawning teleosts, this assumption may seem reasonable, however the reproductive strategy of sharks is often considered more similar to mammals and birds rather than other fish (Wourms, 1977). Mating behaviour has only been observed in the wild for a few species of large shark such as the nurse shark, *Ginglymostoma cirratum* (Bonnaterre 1788) (Klimley, 1980; Carrier *et al.*, 1994), yet there are a number of features of the elasmobranch reproductive strategy that suggest that male fertility may be relatively low.

Firstly, observations of elasmobranch mating suggest that it is typically time consuming and energetically demanding (Castro *et al.*, 1988). Secondly, mating in sharks often involves multiple males, possibly to increase mating success (Pratt and Carrier, 2005) and this may imply that mating success is inherently low. Thirdly, mating is an aggressive activity in elasmobranchs with both sexes inflicting bites on each other during mating (Gilmore *et al.*, 1983), suggesting that the act of copulation itself can lead to mortality. Finally, elasmobranchs have relatively larger brain to body mass ratios (Northcutt, 1977) and there is evidence for complex social hierarchies and behaviour that may be important in terms of reproduction (Gordon, 1993; Jacoby *et al.*, 2010). Other, more subtle mechanisms could also limit the fertility of males. For example, fertilisation in elasmobranchs is internal, and copulation in males occurs via the use of claspers, the paired intromittent organs (Jones *et al.*, 2005). To assist in fertilisation, claspers are equipped with ridges, hooks and barbs, and these may be worn down by use (Pratt and Carrier, 2005), potentially limiting male fertility. It is difficult if not impossible to predict how these specific features of elasmobranch reproduction may affect population dynamics following manipulation of the sex ratio, yet it is clear that males are limited in their capacity for reproduction and that like females, they may also have relatively low fecundities. Hence the assumption of the population model that males have an infinite capacity to inseminate females is probably unrealistic.

Speculating on the nature of the male stock-recruitment relationship is unlikely to be constructive given the paucity of data on male fertility in elasmobranchs, but examples of male-biased harvesting in other taxa suggest that there may be a plethora of direct and indirect effects on population dynamics. Modelling the effects of male-biased game ranching and trophy hunting of impala shows the potential for a population collapse due to social disruption and limitations of male fertility at different ages (Ginsberg and Milnergulland, 1994). Male-biased hunting of grizzly and polar bears may also lead to a lack of sexually mature males in the population (McLoughlin *et al.*, 2005). Among ungulate populations, even when sex-ratios are heavily skewed towards females, male fertility is unlikely to be a limiting factor, but reduced numbers of males can lead to other effects (Mysterud *et al.*, 2002). These include less synchronous breeding and delayed conception in females resulting in lower survival of young born out of season. Other undesirable demographic 'side-effects' observed in terrestrial mammals due to male-biased harvesting include altered sex-ratios of offspring and changes to fecundity (Milner *et al.*, 2007). The consequences of male-biased harvesting are not limited to taxa with internal fertilisation and 'k-selected' life histories; reproductive output in mud crabs was also predicted to be lower due to selective removal of large males (Pillans *et al.*, 2005).

Although sex-differential harvesting among elasmobranchs is common, there are few, if any empirical observations about how targeting males actually impacts population dynamics. Catch records from most fisheries where sharks are encountered are notoriously poor, and even if data is recorded to species level, sex is often not recorded. Some of the best inferences may therefore come from fishery-independent data sets. In the northwestern Atlantic data from the NMFS Cooperative Shark Tagging Program showed a significant decline in both abundance (80% reduction) and maximum size captured (270 to 210 cm FL) in male but not female blue sharks, *P. glauca* (Simpfendorfer *et al.*, 2002a). Given the greater prevalence of males in the region, high levels of fishing might be expected to affect males more than females, potentially explaining the decreases in abundance and length of males. Differing trends in mean size at capture of some species in the KwaZulu-Natal bather protection program e.g. *Carcharhinus brevipinna* (Müller & Henle 1839), *S. lewini* also potentially signal that males and females are affected differently by local fisheries (Dudley and Simpfendorfer, 2006). Although scrutinising similar datasets may potentially provide some evidence of sex-differential harvest, demonstrating its effects conclusively is likely to be a difficult task.

In the Indo-Australian region the only long-term stock assessment of hammerheads (*S. lewini* and *Sphyrna mokarran* grouped), based on data from the Queensland Shark Control Program, suggests that populations may be declining off eastern Australia (de Jong, 2009). If *S. lewini* is declining off eastern Australia, it could potentially be due to a reduction of males by coastal fisheries. However, as the location of the adult female component of the Australian stock is undefined (Chapter 4), and is likely to be shared with nearby countries (Ovenden *et al.*, 2009), declines may also be due to high levels of fishing in other areas. Off eastern Australia the partially aseasonal reproductive cycle reported for *S. lewini* could also be due to a reduction in males leading to a protracted breeding season. Aseasonal reproduction may, however, be a natural feature of the population as it has been reported in *S. lewini* and other shark species (Clarke, 1971; Wourms, 1977).

In conclusion, the demographic modelling carried out in this study showed that male-biased harvesting may potentially provide a way of increasing the yield from harvested shark populations. This can be achieved through restricting harvest to small number of female age classes, enabling higher levels of fishing mortality than the population as a whole can usually sustain, and fishing in areas where males are more common. The scale at which sex-segregation occurs along with the strong size and age-specific habitat preferences of large sharks means the development of sex-biased management strategies is probably feasible. Yet the importance of males to population dynamics should not be underestimated, and manipulating the demography of a population to achieve higher yields may have catastrophic consequences. Given the extremely limited knowledge of male reproductive behaviour and fertility in elasmobranchs, actively initiating sex-biased harvest schemes is fraught with risks. Sex-biased harvesting probably occurs to some extent in most fisheries already. Such fisheries may provide an opportunity to help better understand the role of males in population dynamics and demonstrate whether sex-biased harvesting can indeed be used as a viable management and conservation strategy.

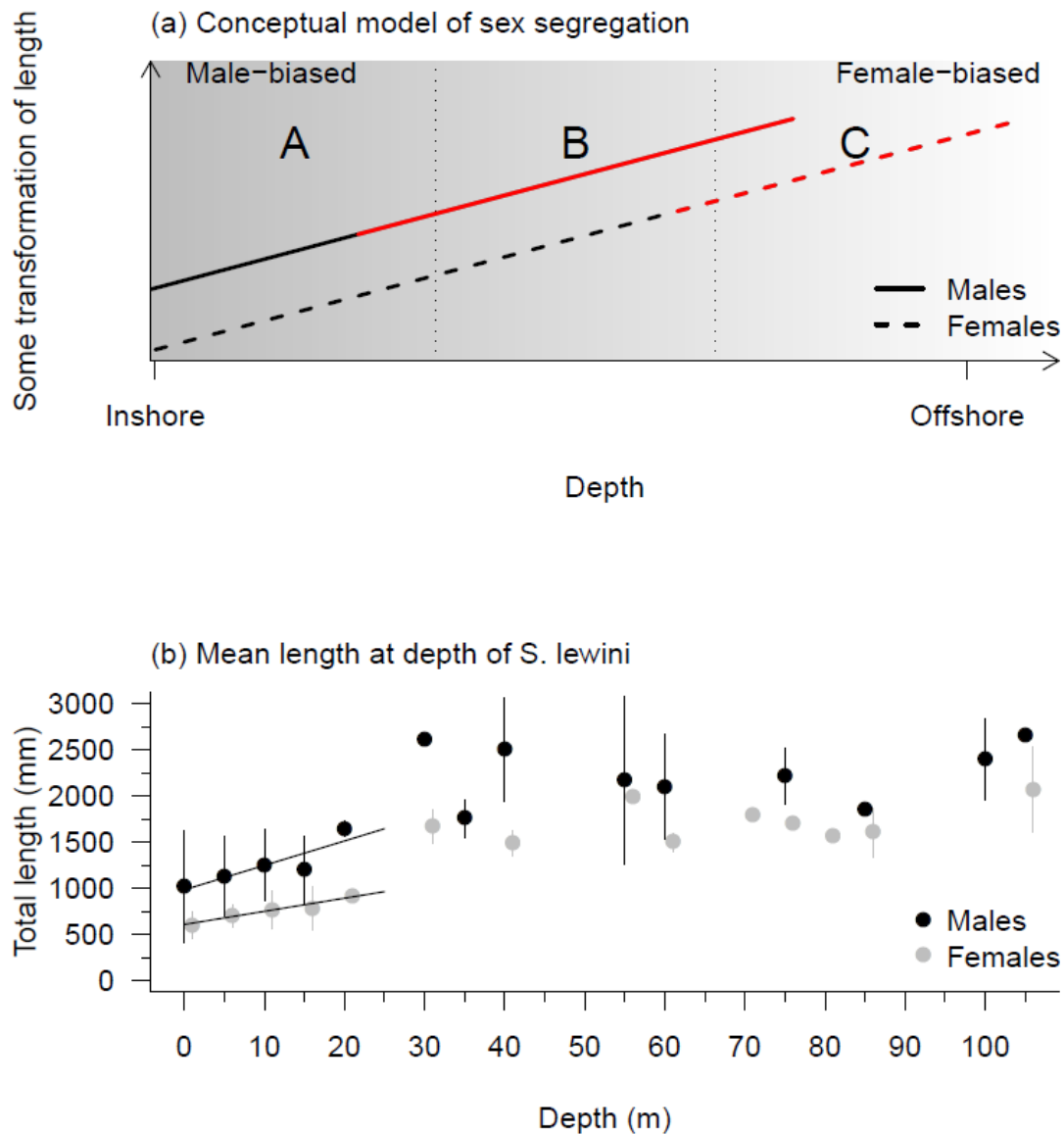


Figure 7.1 Conceptual model of sexual segregation for *Sphryna lewini* (a), showing how the length of an individual is a function of depth, and that this varies by sex. Red components represent mature individuals. Mean length-at-depth information for *S. lewini* in coastal waters off eastern Australia is used to provide an empirical illustration of the model (b). In waters <25m depth the relationship appears to be non-linear.

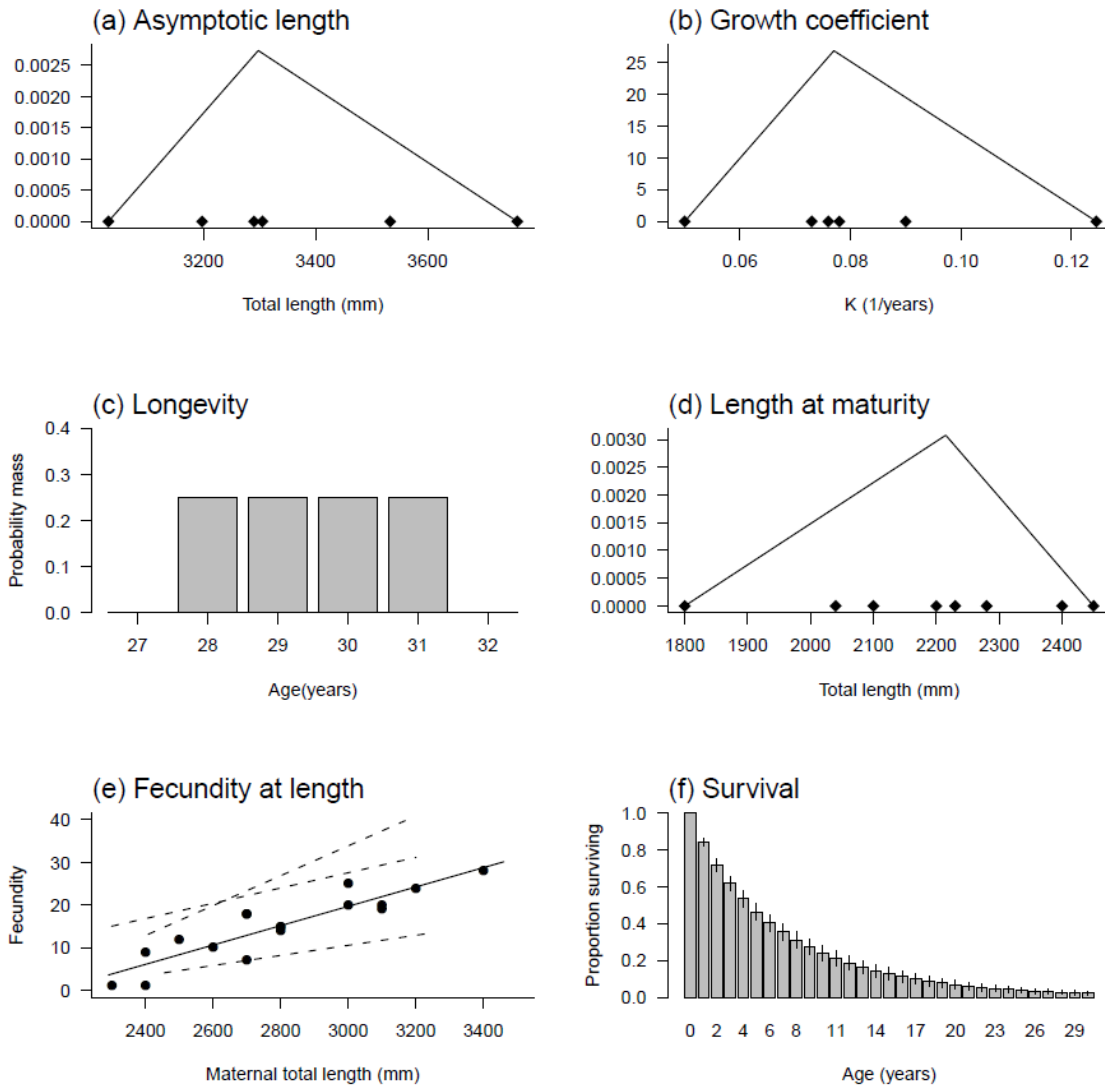


Figure 7.2 Statistical distributions and values of life history parameters used to create a stochastic, age structured population model for *Sphyrna lewini*. Black diamonds in (a,b and d) represent observed values of life history parameters from the primary literature. Black circles in (e) are observed data points used to establish the relationship between maternal length and fecundity in eastern Australian waters, while dashed lines represent published relationships of fecundity for *S. lewini* from other parts of the world. Mean age-specific survival (\pm s.d.) is given in (f).

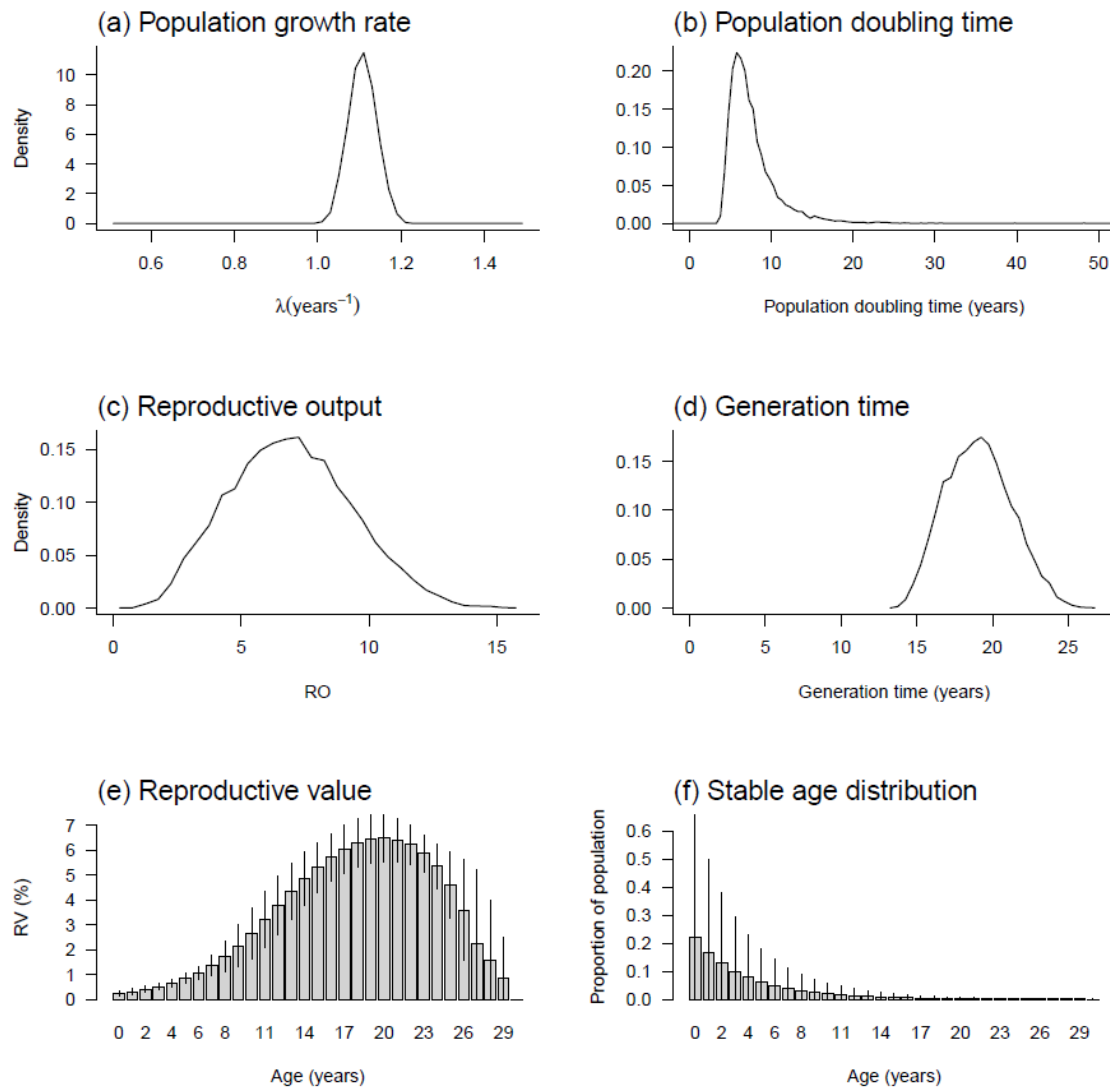


Figure 7.3 Statistical distributions of demographic parameters for unharvested *Sphyrna lewini* using Monte Carlo simulation run 1000 times. Error bars in (e) and (f) are one standard deviation.

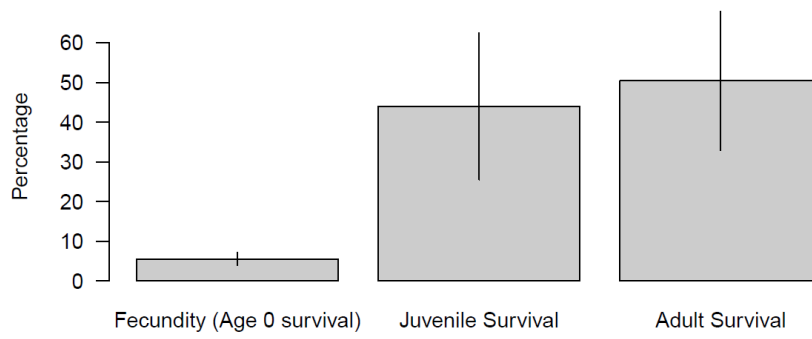


Figure 7.4 Mean fecundity, juvenile survival and adult survival elasticities from 1000 population models of *Sphyrna lewini*. Error bars are one standard deviation.

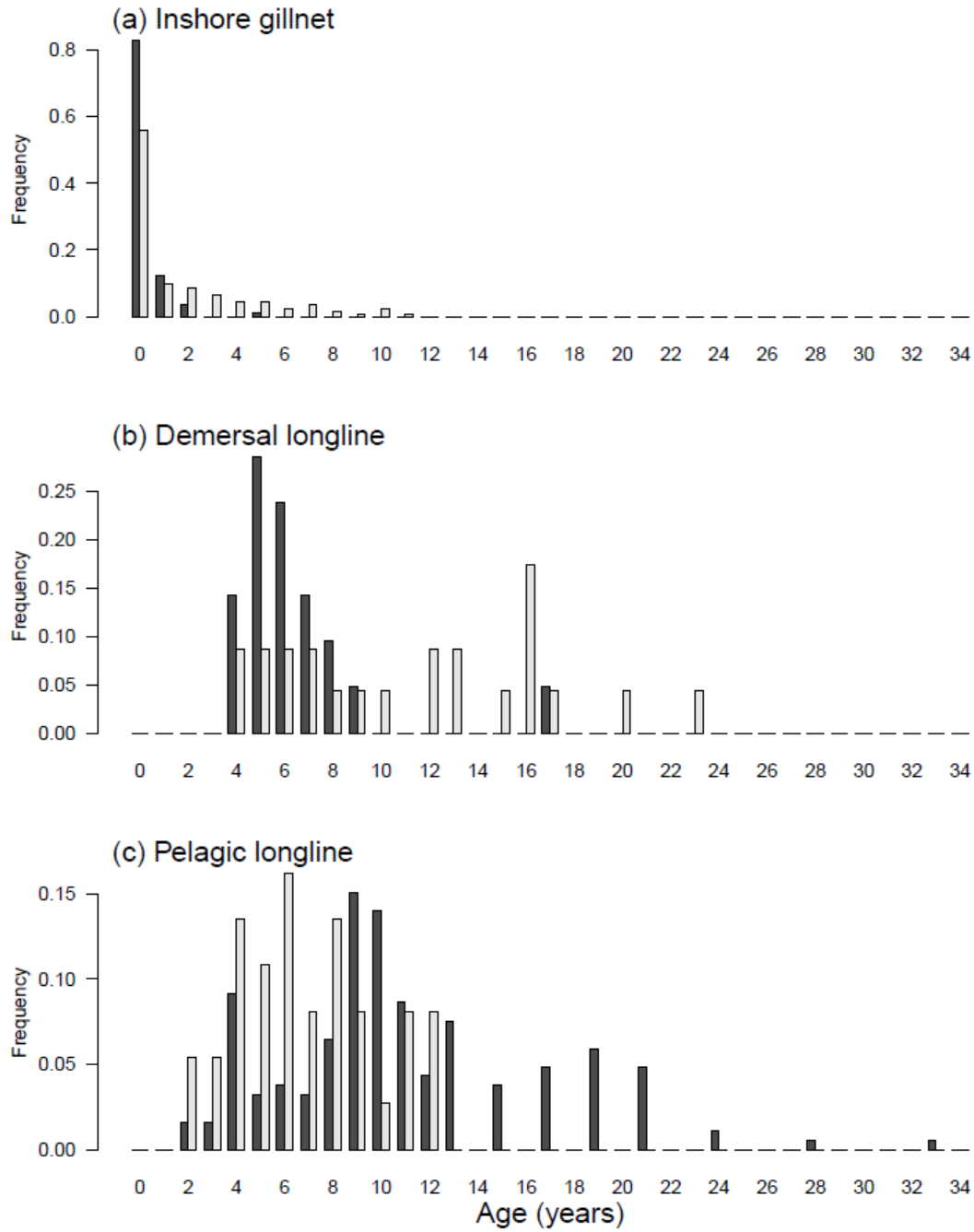


Figure 7.5 Age-frequency histograms for males (light grey) and females (dark grey) showing age classes of *Sphyrna lewini* available to three commercial fisheries in the Indo-Australia region.

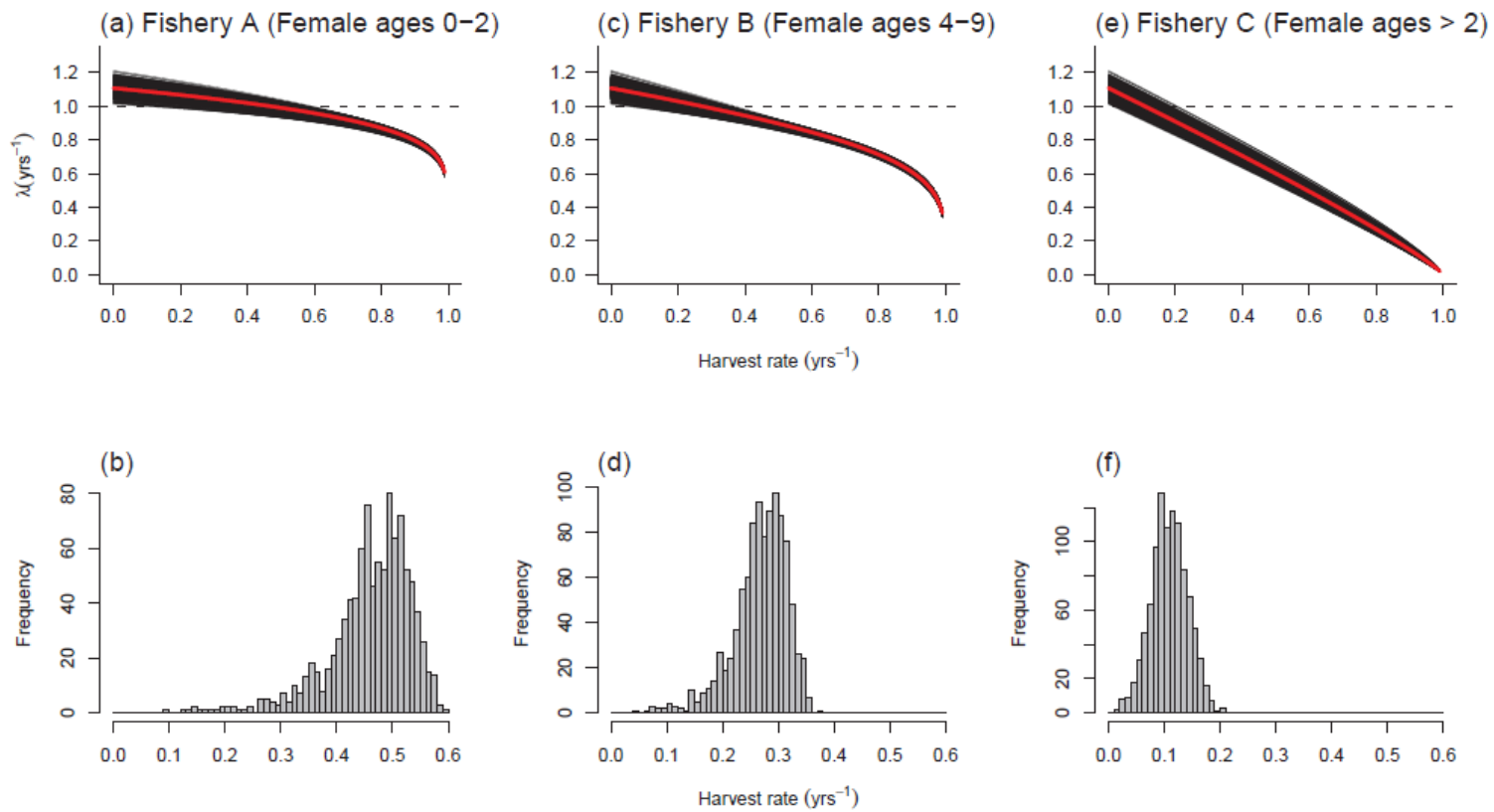


Figure 7.6 Response of population growth rate to harvest levels between 0 and 1 in three fishery scenarios (Table 2.3). Red lines indicate the mean value based on 1000 Monte Carlo simulations. Horizontal lines ($\lambda = 1$) indicate when population growth rates becomes negative.

Table 7.1 Values for life history parameters used to create demographic models for scalloped hammerhead, *Sphyrna lewini*.

<i>Parameter</i>	<i>Symbol</i>	<i>Unit</i>	<i>Distribution</i>	<i>Median/mean</i>	<i>Min</i>	<i>Max</i>
Growth coefficient	k	years ⁻¹	Triangular	0.077	0.05	0.125
Length at birth	L_0	mm	-	-	-	-
Asymptotic length	L_∞	mm	Triangular	3301	3030	3640
Length-at-maturity	L_{MAT}	mm	Triangular	2215	1800	2450
Maximum age	A_{MAX}	years	Uniform	-	28	31
Sex ratio (M/F)	-	-	-	1:1	-	-
Linear model fecundity-at-length	a	-	-	0.0227	-	-
Linear model fecundity-at-length	b	-	-	-48.26	-	-
Reproductive periodicity	-	year	-	1	-	-
Power model weight-at-length	a	-	-	3.22E-09	-	-
Power model weight-at-length	b	-	-	3.048	-	-

Table 7.2 Estimates of mortality rates (yr^{-1}) from seven empirical methods

Type	Method	Mean	Min	Max	Mean Age 0	Mean Age 31
Age independent	Hoenig 1983 (Teleost)	0.141	0.130	0.149		
	Hoenig 1983 (Cetacean)	0.134	0.128	0.140		
	Hoenig 1983 (Combined)	0.152	0.145	0.160		
	Pauly 1980	0.094	0.067	0.123		
	Jensen 1996	0.080	0.166	0.300		
Age dependent	Peterson and Wroblewski 1984	0.095	0.083	0.113	0.236	0.067
	Chen and Watanabe 1989	0.148	0.105	0.200	0.477	0.093

Table 7.3 Description of three fishery scenarios and the level of harvest (plus confidence intervals) required by each one to maintain a stationary population growth rate

Fishery	Location	M/F sex ratio	Vulnerable age classes		Stationary harvest fishing level (yr ⁻¹)		
			Males	Females	Mean	Lower CI	Upper CI
A: Inshore gillnet	Eastern Australia (tropics)	1.9:1	0-10	0-2	0.455	0.261	0.561
B: Mid-shelf, demersal longline	Eastern Australia (sub tropic)	1:1	4-max	4-9	0.264	0.14	0.339
C: Pelagic longline	Indonesia	1:5	2-max	2-max	0.106	0.042	0.171

Chapter 8. General discussion



Plate 8. Sunset at rattlesnake island (December 2008)

8.1 THE ROLE OF LIFE HISTORY STUDIES IN MANAGING SHARK POPULATIONS

The challenges faced in managing the Queensland East Coast Inshore Finfish Fishery are shared by similar shark fisheries throughout the tropical regions of the world. Small-scale coastal fisheries such as the ECIFF present a number of unique difficulties in terms of sustainable management and exploitation (Chapter 2). Coastal ecosystems are complex and dynamic, and this has direct consequences in shaping the biology of resident species (Knip *et al.*, 2010). The diversity of sharks occurring in such areas is typically high (Musick *et al.*, 2004) (Chapter 2), and the captured species display a range of life history characteristics (Chapter 3, Chapter 4), as well as complex spatial behaviours and habitat preferences (Heupel *et al.*, 2007; Knip *et al.*, 2010). Recently discovered phenomena such as hybridisation are likely to further complicate management (Chapter 5) (Morgan *et al.*, In review). In addition to the biological issues associated with these fisheries, there are also a range of socio-economic challenges including their inherently low value, difficulty to monitor and regulate, and high accessibility to humans.

In recent decades scientists have developed a number of tools to combat the difficulties of working with data-limited fisheries. These range from qualitative risk assessments frameworks (Stobutzki *et al.*, 2002; Chin *et al.*, 2010) to semi-quantitative risk assessments incorporating some population dynamics (Blaber *et al.*, 2009), to fully quantitative population dynamic and stock assessment models (Cortés, 2007). Many of these have been developed specifically for use with elasmobranchs (Forrest and Walters, 2009; Brooks *et al.*, 2010) and some specifically address the problems associated with tropical shark fisheries (Gallucci *et al.*, 2006). Comparative life history and demography studies have also attempted to bridge the knowledge gap between elasmobranch and teleost research and can offer useful insights that may be applicable to the conservation and management of shark populations (Smith *et al.*, 1998; Cortés, 2000; Frisk *et al.*, 2001; Cortés, 2002; Dulvy and Reynolds, 2002; Mollet and Cailliet, 2002; Frisk *et al.*, 2005; Cope, 2006; García *et al.*, 2008). Many of the above tools are underpinned by strong theoretical foundations and draw on principles that have been established in better-studied taxonomic groups (Beverton and Holt, 1959; Charnov and Berrigan, 1991; Caswell, 2001). However dire the predictions of global fisheries may become (Pauly *et al.*, 2005; Jackson, 2008; Worm *et al.*, 2009), the ever-increasing sophistication of our models and the growing movement toward conservation of elasmobranchs (Dulvy *et al.*, 2008) provides considerable cause for optimism; somewhere between extinction and carrying capacity there exists a point where a population can

fulfil both its ecological functions and satisfy human demand, and scientists have the ability to find that point.

While our models may be capable of predicting outcomes in situations where data are unavailable, they are of course, still reliant on some data for their creation. Outside the range of the data, we can only extrapolate. Hence the capacity of our models to successfully predict the outcome of a situation is entirely limited by the quality and existence of data at some level. As such, the paucity of accurate life history data available for many elasmobranchs may now be one of the biggest impediments to successful conservation and fisheries exploitation. Interestingly, research growth in the fields of elasmobranch fisheries and conservation biology has largely coincided with the personal computing revolution. It is perhaps not surprising that the development of computer intensive methods for managing elasmobranch populations (which now only requires access to a library and a desktop computer) has now outpaced the collection of data itself. It is in this context, the provision of life history data, that the contribution and significance of this PhD thesis should be viewed.

This PhD thesis provides a contribution to the life history of several species of shark that are commercially captured on the east coast of Queensland. In addition to being commercially utilised in Queensland and northern Australia, most are also harvested throughout their range globally (Blaber *et al.*, 2009; White and Kyne, 2010). The most comprehensive life history data are provided in Chapter 6 for the Australian blacktip shark, *Carcharhinus tilstoni*, and the spot-tail shark, *Carcharhinus sorrah*. These species are the largest components the ECIFF both in terms of weight and number (Chapter 2). Chapter 6 presents the relationships between length and the variables weight, fecundity, maturity and maternity, as well as the length-at-age relationship for these species. Validation studies confirm both the accuracy of the ageing method used and longevity of these species, allowing a high degree of confidence in these results (Davenport and Stevens, 1988; Stevens *et al.*, 2000b).

The first detailed age and growth information are also presented for three additional commercially important species in the ECIFF: the milk shark, *Rhizoprionodon acutus* (Chapter 3), the scalloped hammerhead, *Sphyrna lewini* and the great hammerhead, *Sphyrna mokarran* (Chapter 4). In addition to the data presented on the above five species, data were opportunistically collected from all other species encountered during fishery-dependent and fishery-independent activities. These include lesser-studied species such as *Carcharhinus*

fitzroyensis, *Carcharhinus macloti*, and *Eusphyra blochii*, for which basic life history data (e.g. age and growth) have not previously been established anywhere in their range globally.

A summary of all life history data presently available for the elasmobranchs captured by the ECIFF within the GBRWHA is provided as an online appendix to this thesis ([Appendix 2: Queensland East Coast Shark data](#)) and is also available as an [excel spreadsheet](#). This list includes all species encountered during onboard-vessel observer surveys (Table 2.3). [Appendix 2](#) includes all data gathered directly from this thesis, as well as presently unpublished data collected opportunistically (e.g. length-weight relationships), and data obtained from the primary literature. The content is presented online so that it may be available immediately and is colour-coded to help identify knowledge gaps and species that should be a priority for future research.

Considerable progress has now been made towards obtaining at least basic information on vital rates for most species caught by the ECIFF ([Appendix 2](#)); data specific to Queensland are now available for many species, and there is relevant data from Australia for most species. The completion of several student projects currently underway will further address knowledge gaps on key species in the ECIFF such as *Carcharhinus melanopterus* (A. Chin, JCU), *Loxodon macrorhinus* (A. Gutteridge, UQ), *G. cuvier* (B. Holmes, UQ), *C. limbatus* and *C. brevipinna* (P. Geraghty, Macquarie) and several rhynchobatid species (J. White, JCU). Areas where there is specific need for more data include determining the size and age at maternity for the majority of species. Knowledge of the age at which animals actually begin reproducing, as distinct from maturing, can be used to improve the accuracy of population models (Walker, 2005b). This is evident for *C. tilstoni*, where age-at-maternity occurred approximately two years after age-at-maturity (Chapter 6). The relationship between maternal length and fecundity is also unknown for many species in the ECIFF and is important to maximise the accuracy of population models.

8.2 FISHERY IMPLICATIONS AND RECOMMENDATIONS

The direct implications of this PhD study are an improved knowledge of the sharks that are commercially exploited in the waters of the GBRWHA. This data can be used to improve the management of harvested shark species by providing relevant information for risk assessments and population assessments. Data from the project has already been used in a risk assessment for the ECIFF (Tobin *et al.*, 2010). If levels of fishing mortality can be established for the focal species of the fishery, *C. tilstoni* and *C. sorrah*, the data presented in Chapter 6 are sufficient to

develop age-structured population models to predict population trends. This approach has been used in the management of sharks in other parts of Australia (Simpfendorfer, 1999; McAuley *et al.*, 2007a). For species such as the hammerheads, while life history data are less comprehensive, they can be used to give an indication of the potential response to fishing pressure in hypothetical situations (e.g. Chapter 7).

While the results of this research cannot be used to speculate on the status of individual species or on the sustainability of sharks caught by the ECIFF, some observations can be made on the characteristics of the fishery and its captured species. These may provide a context for evaluating the threats and shaping future research priorities. From a historical perspective, the commercial catch of sharks within the GBRWHA has been relatively low (<1500 tonnes.yr⁻¹) (Gribble *et al.*, 2005) and unlike other parts of northern Australia it was not fished intensively by the large-scale Taiwanese gillnet and longline fishery that operated during the 1970s and 1980s (Walter, 1981; Stevens and Davenport, 1991). In addition to this, 33% of the GBRWHA has been protected from commercial fishing since 2004 (GBRMPA, 2009), and this is likely to provide some protection to resident shark species. The recent introduction of stricter input and output controls on the ECIFF, along with clearer definition of the shark component of the fishery, and reduction of latent effort within the fishery are also likely to reduce fishing pressure on sharks in the future. The results of this PhD study also affirm the notion that many tropical sharks captured by the ECIFF are relatively productive in comparison to shark species occupying other habitat types. For instance, many of the species captured by the ECIFF have relatively high rebound potentials in comparison to elasmobranchs occupying deepwater and temperate habitats (Figure 8.1, Table 8.1) (Smith *et al.*, 1998; Simpfendorfer and Kyne, 2009) – although reef sharks may be an exception (Robbins, 2006).

These factors suggest that the GBRWHA should be well-placed to become a sanctuary for Indo-Pacific elasmobranch biodiversity. Unprecedented targeting of elasmobranchs in nearby countries such as Indonesia (White and Kyne, 2010) will further increase the relevance of such a sanctuary as regional stocks are depleted. Yet, recent reports of dramatic declines in some species within the GBRWHA (Robbins *et al.*, 2006; de Jong, 2009) are concerning at several levels. Not only do they suggest that historical declines have already occurred in the GBRWHA, but they also risk permanently undermining scientific and public perception of the GBRWHA as an effective model for conservation and management. Perhaps the most immediate need within the GBRWHA is therefore the development and implementation of long-term monitoring programs that can be

used to establish trends in abundance of resident shark species. Designing appropriate monitoring programs where data from fisheries are extremely limited can be facilitated through an appreciation of the life history characteristics of resident species (Chapter 2).

Among the sharks found within the GBRWHA and occurring within the ECIF (Table 2.3), the large-coastal species and hammerheads (Table 2.6) appear to have lower capacity to recover after fishing (Figure 8.1, Table 8.1) and therefore should be a priority for monitoring. These species display characteristics such as large size, late age-at-maturity, biennial reproduction and high longevity. Their greater size and mobility also places them at a higher risk of capture if they migrate outside of the GBRWHA; indeed genetic connectivity with nearby countries (e.g. Indonesia) has already been demonstrated for some species (Ovenden *et al.*, 2009). Yet monitoring of these species can be facilitated surprisingly easily; all are captured in the Queensland Shark Control Program (QSCP), thereby providing a fishery-independent measure of abundance using standardised, year-round effort. Data from a similar bather protection program has been successfully used to evaluate the population status of large sharks in South Africa (Dudley and Simpfendorfer, 2006) and can also provide an invaluable source of long-term life history data for rare and difficult to study species (Cliff, 1995; de Bruyn *et al.*, 2005; Hussey *et al.*, 2010). The recent development of cost-effective methods of identifying individuals based on their fins overcomes the major logistical difficulties associated with collection of data from such programs, as sharks can be accurately identified, measured and sexed *in situ* by simply photographing their fins without any need to retain samples or specialised training of contactors (Marshall, 2011).

8.4 FUTURE RESEARCH DIRECTIONS

At a broader level, despite the development of standard protocols for studies of growth and reproductive biology (Walker, 2005b; Cailliet *et al.*, 2006), there is still a clear need for more life history studies as well as the ongoing development and refinement of current methodologies. The limitations of our knowledge with respect to shark life histories are still patently clear. Even among well-studied families such as the Carcharhinidae and Sphyrnidae there are apparent inconsistencies in life history data that seem to be, at least partly, if not wholly driven by methodological issues. These include, for example, the discrepancy in maximum age of *S. lewini* (Chapter 4), which may be due to methodological differences between studies. Many growth studies of sharks also fail to display asymptotic growth (Braccini *et al.*, 2007; Francis *et al.*, 2007)

(Chapter 6) suggesting either systematic underestimation of longevity among this taxa or fundamental flaws in our understanding of growth and natural mortality in sharks. For example, the existence of a triennial reproductive cycle in *G. cuvier* (Whitney and Crow, 2007) – a feature of long-lived species– is difficult to reconcile with the relatively low maximum ages (11-22 years) so far reported for this species (Natanson *et al.*, 1999; Wintner and Dudley, 2000; Kneebone *et al.*, 2008). The recent separation of *Squalus suckleyi* as distinct from *Squalus acanthias* is also a reminder that inconsistencies in life history may also be caused by taxonomic differences (Lavery and Shaklee, 1991; Ebert *et al.*, 2010).

Two specific areas of elasmobranch life history requiring further attention are age validation and survival. Despite the regular appearance of papers stressing the importance of age validation (Campana, 2001; Cailliet *et al.*, 2006), it is still frequently neglected. The most commonly used method, chemically marking the vertebrae and releasing sharks into the wild is time consuming, costly and often requires large sample sizes for success. Hence, it is most suited for targeted shark fisheries or long-term projects (Simpfendorfer *et al.*, 2002b; McAuley *et al.*, 2006). Greater use of validation methods such as bomb radiocarbon dating that require few samples and validate a wide range of age-classes (Campana *et al.*, 2002; Passerotti *et al.*, 2010) should be encouraged along with development of novel methods and application of existing techniques (e.g. radiochemical dating) used for teleosts to elasmobranchs. In addition to studies validating age, there is also a need for studies that attempt to measure survival in wild shark populations. At present, empirical estimates of survival in elasmobranchs are limited to only a few studies (Gruber *et al.*, 2001; Heupel and Simpfendorfer, 2002; In press). As a result there is currently an overreliance on indirect methods for estimating mortality that have been developed for use with other taxa. Given the importance of survival in population models, more studies should specifically attempt to measure survival, especially among young-of-the-year individuals.

Ultimately, life history data will continue to play an important role in developing sustainable management practices for shark fisheries. While there has been an increased awareness of the importance of life history studies on chondrichthyans in recent years, there is clearly still much to be learned (Simpfendorfer *et al.*, 2011). There are still a numbers of families for which only scant information is available (e.g. Chimaeridae, Scyliorhinidae) and many habitats for which only basic information is known (e.g. deepwater and freshwater). As further study is carried out on this poorly known class of animals, it will almost certainly provide an insight into the adaptations that

have shaped their diversity and led to their successful persistence as apex predators in aquatic ecosystems over the past 400 million years.

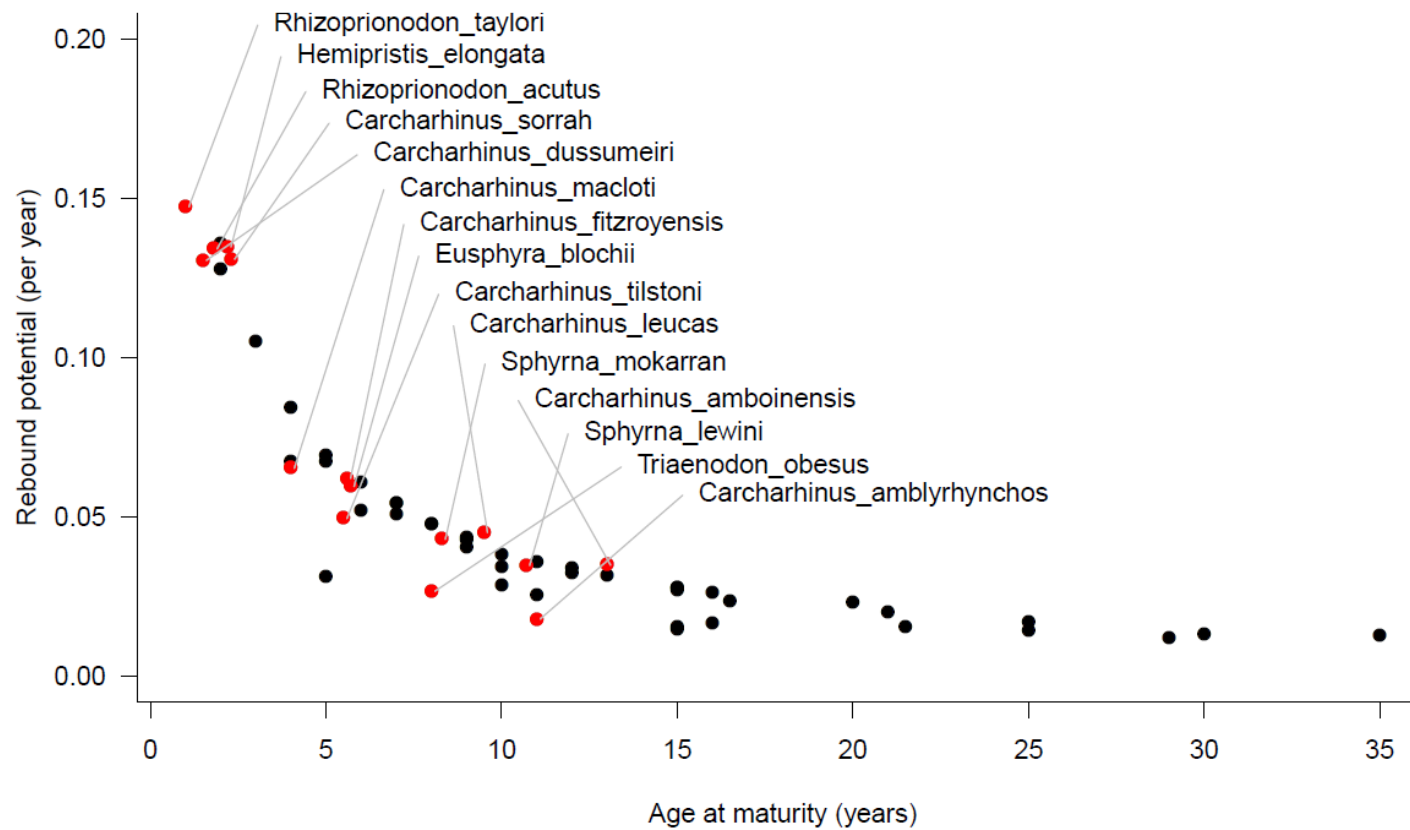


Figure 8.1. Intrinsic rebound potential (r_{2M}) of sharks caught by the Queensland East Coast Inshore Finfish Fishery as a function of age at maturity. Black points represent rebound potentials calculated for other species from Smith *et al.* (1998) and Simpfendorfer and Kyne (2009).

Table 8.1 Intrinsic rebound potential of sharks caught in the Queensland East Coast Inshore Finfish Fishery. α is age at 50% maturity, w is maximum longevity, b is mean number of female pups born annually, M is natural mortality based on the method of Jensen 1996 ($1.6k$), $l_{\alpha 2M}$ is survival to maturity when survival = $2M$, and r_{2M} is intrinsic rebound potential (at $1.00b$). Data are sorted by decreasing r_{2M} values.

Species	α	w	b	M	$l_{\alpha 2M}$	r_{2M}
<i>Rhizoprionodon taylori</i>	1	7	2.25	1.621	0.427	0.147
<i>Hemipristis elongata</i>	2.2	15	1.5	0.501	0.422	0.135
<i>Rhizoprionodon acutus</i>	1.8	8.1	1.55	1.008	0.559	0.134
<i>Carcharhinus dussumieri</i>	1.5	6.5	1	1.302	0.926	0.130
<i>Carcharhinus sorrah</i>	3.3	13.7	1.5	0.517	0.430	0.101
<i>Carcharhinus macloti</i>	4	12	0.5	0.413	1.000	0.065
<i>Carcharhinus fitzroyensis</i>	5.6	12.5	2.3	0.304	0.200	0.062
<i>Eusphyra blochii</i>	5.7	21	5.9	0.186	0.053	0.059
<i>Carcharhinus leucas</i>	9.5	27	1.75	0.253	0.227	0.045
<i>Sphyrna mokarran</i>	8.3	39	3.33	0.126	0.067	0.043
<i>Carcharhinus tilstoni</i>	7.4	18	1.9	0.131	0.128	0.039
<i>Carcharhinus amboinensis</i>	13	30	2.25	0.232	0.165	0.035
<i>Sphyrna lewini</i>	10.7	31	7.55	0.123	0.029	0.035
<i>Triaenodon obesus</i>	8	19	0.5175	0.080	0.335	0.027
<i>Carcharhinus amblyrhynchos</i>	11	19	0.75	0.080	0.258	0.018

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Appendix 1. Protocol used to distinguish between two species of morphologically similar blacktip sharks

Identification methods were applied sequentially. When an individual met the necessary conditions of one method, it was considered identified. STL is stretch total length in mm and PCV is pre-caudal vertebrae

Order applied	Identification method	Necessary conditions		Justification
		<i>C. tilstoni</i>	<i>C. limbatus</i>	
1.	Pre-caudal vertebrae counts	PCV in the range of 83-91	PCV in the range of 94-110	Identifications of 196 post-natal individuals using vertebral counts were consistent with differences between <i>C. tilstoni</i> and <i>C. limbatus</i> in length-at-birth, male clasper length, and male and female reproductive stage.
2.	Life history characteristics	STL <652 mm	STL > 665 mm, unhealed umbilical scar	From vertebral counts of 108 neonates. 652 mm is the empirically derived 97.5 th quantile of the length-at-birth distribution for <i>C. tilstoni</i> and 665 mm is the empirically derived 2.5 th quantile of the length-at-birth distribution for <i>C. limbatus</i> .
		Male, STL <1620 mm, sexually mature	Male, STL > 1300 mm, sexually immature	Based on the reproductive stage of 372 males. 1620 mm was the largest male. 1300 mm is a conservative, non-statistically derived estimate of the length at which 95% of males <i>C. tilstoni</i> are mature.
		Male, STL >1000 mm and <1300 mm, clasper length >4% of STL	Male, STL >1200 mm and <1300 mm, clasper length <4% of STL	Based on the clasper length of 361 males. 1000 - 1300 mm is the length over which rapid elongation (and calcification) of claspers occurred in male <i>C. tilstoni</i> . Claspers of <i>C. limbatus</i> remain undeveloped (<4% STL) until at least 1600 mm.
		Female, STL < 1930 mm, sexually mature	Female, STL > 1400 mm, sexually immature	Based on the reproductive stage of 183 females. 1930 mm is the largest female measured. 1400 mm is a conservative, non-statistically derived estimate of the length at which 95% of female <i>C. tilstoni</i> are mature.
3.	Molecular analysis	PCR melt temperature within the range of 76.5 - 77.5°C with a mean of 77.0°C	PCR melt temperature within the range of 79.5 - 81.0°C with a mean of 80.3°C	Identification using a real-time, high resolution melt polymerase chain reaction species-diagnostic assay developed from the ND4 gene and validated against vertebral counts of 96 post-natal <i>C. tilstoni</i> and <i>C. limbatus</i> . This method does not distinguish between hybrid animals, so the overall accuracy is approximately 85%.

